

The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia

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Contents

Synopsis	175
Introduction	176
Lettering used in text figures	177
Systematic descriptions	181
Family Stegotrachelidae Gardiner	181
Genus <i>Mimia</i> Gardiner & Bartram	181
<i>Mimia toombsi</i> Gardiner & Bartram	181
Genus <i>Moythomasia</i> Gross	181
<i>Moythomasia durgaringa</i> Gardiner & Bartram	182
Neurocranium: general features	182
Occipital region	185
<i>Mimia toombsi</i>	185
<i>Moythomasia durgaringa</i>	199
Occipital region: discussion	201
1. Posterior dorsal fontanelle	201
2. Occipital fissure	203
3. Vestibular fontanelle	203
4. Ventral otic fissure	204
5. Supraoccipital	206
6. Aortic canal	206
7. Canal for abducens nerve	207
8. Zygial plates	207
9. Occipital artery	207
10. Segmental structure of occiput	208
11. Longitudinal intervertebral ligament	210
Otic and orbitotemporal regions	210
Review of ossification centres	210
<i>Mimia toombsi</i>	215
<i>Moythomasia durgaringa</i>	228
Otic and orbitotemporal regions: discussion	231
1. Parampullary process	231
2. Articulation of first suprapharyngobranchial	233
3. Articulation of first infrapharyngobranchial	234
4. Lateral commissure and trigeminofacialis chamber	235
(a) Actinopterygians	236
(b) Osteichthyans	238
(c) Gnathostomes	239
5. Hyomandibular facet	240
6. Otic-sphenoid fissure	241
7. Fossa bridgei and lateral cranial canal	241
8. Spiracle and spiracular canal	243
9. Origin of dorsal hyoid constrictor muscle	244
10. Origin of dorsal mandibular constrictor muscle	245
11. Endolymphatic duct	246
12. Pterosphenoid pedicel	247
13. Prootic bridge and posterior myodome	247

14. Anterior and middle cerebral veins	249
15. Sclerotic bones	251
Ethmoid region and associated dermal bones	254
<i>Mimia toombsi</i>	254
<i>Moythomasia durgaringa</i>	260
Ethmoid region: discussion	264
1. Anterior myodome	264
2. Postnasal wall and nasal capsule	266
3. Dermal bones of the snout	267
Parasphenoid and associated toothplates	271
<i>Mimia toombsi</i>	271
<i>Moythomasia durgaringa</i>	273
Parasphenoid: summary and discussion	273
1. Parabasal canal	275
2. Internal carotid artery	276
3. Basipterygoid process	276
4. Ascending process	277
5. Parasphenoid teeth	278
6. Bucco-hypophysial canal	279
7. Subcephalic muscles	279
8. Accessory toothplates	280
Palatoquadrate and dermal bones of the cheek	280
<i>Mimia toombsi</i>	280
<i>Moythomasia durgaringa</i>	292
Palatoquadrate: summary and discussion	293
1. Palatoquadrate commissure and vomer	293
2. Anterior articulation	297
3. Otic process and palatobasal articulation	298
4. Otic process and prespiracular cartilage	301
5. Ossifications of the palatoquadrate	305
(a) Cartilage bones	305
(b) Dermal bones	306
(c) Ectopterygoid	307
(d) Dermopalatines	307
(e) Entopterygoid	308
(f) Dermometapterygoid	310
Dermal bones of cheek: summary and discussion	310
Sensory canals of cheek: summary and discussion	313
Dermal bones of the skull roof	316
<i>Mimia toombsi</i>	316
<i>Moythomasia durgaringa</i>	318
Dermal bones of skull roof: summary and discussion	320
1. Homologies of dermal bones of skull roof	320
2. Sensory canals of skull roof	324
Lower jaw	325
<i>Mimia toombsi</i>	325
<i>Moythomasia durgaringa</i>	331
Lower jaw: discussion	332
1. Meckelian ossifications	332
2. Dermal bones	332
Operculogular series	338
<i>Mimia toombsi</i>	338
<i>Moythomasia durgaringa</i>	339
Operculogular series: summary and discussion	339
1. Branchiostegal rays and gular plates	339
2. Opercular cartilages and opercular bones	342
Hyoid and branchial arches	344
<i>Mimia toombsi</i>	344
<i>Moythomasia durgaringa</i>	349

Hyoid and branchial arches: discussion	349
1. Hyoid arch	349
2. Basibranchial and branchial arches	359
Axial skeleton	363
<i>Mimia toombsi</i>	363
<i>Moythomasia durgaringa</i>	364
Axial skeleton: discussion	364
1. Arcualia	364
2. Centra	365
3. Ribs	366
4. Supraneurals and neural spines	368
Shoulder girdle and pectoral fin	368
<i>Mimia toombsi</i>	368
<i>Moythomasia durgaringa</i>	374
Shoulder girdle and pectoral fin: discussion	374
1. Dermal bones of shoulder girdle	374
2. Endoskeletal girdle	378
3. Pectoral fin	381
Pelvic girdle and fin	382
<i>Mimia toombsi</i>	382
<i>Moythomasia durgaringa</i>	382
Pelvic girdle and fin: discussion	383
Median fins	384
<i>Mimia toombsi</i>	384
<i>Moythomasia durgaringa</i>	385
Median fins: discussion	386
1. Dorsal and anal fins	386
2. Caudal fin	386
Squamation	386
<i>Mimia toombsi</i>	386
<i>Moythomasia durgaringa</i>	387
Squamation: discussion	388
1. Scale structure	388
2. Basal fulcra	392
3. Fringing fulcra	394
Phylogenetic results	394
Interrelationships of actinopterygians	394
Classification	399
Relationships of actinopterygians	400
Acknowledgements	406
References	407
Index	418

Synopsis

Two species of palaeoniscids are described from the Frasnian of Gogo, Western Australia: *Mimia toombsi* Gardiner & Bartram, and *Moythomasia durgaringa* Gardiner & Bartram. A detailed account of their head structure, appendicular and axial skeletons and squamation is given in a series of accounts of regional anatomy. Each account is accompanied by a discussion of the salient features in which comparison is made with living and fossil actinopterygians as well as all other major gnathostome groups. In the course of these comparisons previously-described material of *Cheirolepis*, *Acanthodes*, various placoderms, hybodont sharks and cephalaspids is reinterpreted.

The Western Australian genera are similar in many respects, including the pattern of the dermal bones of the skull, cheek and pectoral girdle. *Moythomasia* has a short, blunt snout with small premaxillae separated by a toothed rostral, and a palatoquadrate with a short anterior ramus. *Mimia* has a longer, hooked snout with large premaxillae which meet in the mid-line, excluding the rostral from the jaw margin, and a palatoquadrate with a long anterior ramus. *Moythomasia* shows one marked advance over *Mimia* in the possession of a rudimentary ascending process on the parasphenoid.

The most striking primitive features of the Gogo palaeoniscids are the incomplete cranial fissure in

which the ventral otic fissure was cartilage-filled and separate from the perichondrally-lined otico-occipital fissure, the presence of a lateral cranial canal, dermohyal, basal and fringing fulcra, a perforated propterygium, and the assumed enclosure of the adductor mandibulae muscle by the palatoquadrate and dermal cheek bones.

The principal anatomical conclusions concern the history of the myodome and trigeminofacial chamber, and the spiracular canal.

The ossification patterns of the skull roof, cheek, palate, lower jaw and shoulder girdle of osteichthyans are reviewed critically. It is concluded that there are two distinct dermal roofing bone patterns and that an operculogular series is a primitive gnathostome attribute whereas submandibulars are a sarcopterygian synapomorphy.

The principal conclusion about the interrelationships of actinopterygians is that the Palaeonisciformes are a paraphyletic group. *Mimia* and *Moythomasia* are stem-group actinopterygians whereas *Cheirolepis* is a basal actinopterygian. Most other palaeoniscids are stem-group neopterygians and may be inserted between the Chondrostei and the Neopterygii.

The principal broader phylogenetic conclusions concern the interrelationships of the sarcopterygians and the relationships of the chondrichthyans and placoderms. The Porolepiformes are considered to be the sister-group of the choanates, the placoderms the sister-group of the osteichthyans and the chondrichthyans the primitive sister-group of other gnathostomes.

Introduction

The first aim of this paper is to make known the palaeonisciform fishes from the Devonian Gogo Formation of Western Australia.

The specimens were mainly collected in 1967 by a joint expedition from the British Museum (Natural History), the Western Australian Museum and the Hunterian Museum, Glasgow (Brunton, Miles & Rolfe 1969; with references) at Gogo Station, a cattle property some 250 km SE of Derby in the Fitzroy Trough. The Fitzroy Trough lies on the northern flank of the Canning Basin, with its northern limit faulted against the Kimberley Plateau, a stable Precambrian block (Playford & Lowry 1966). The Canning Basin was apparently land during the Middle Devonian, with a southern shore-line near its junction with the Kimberley Plateau. In the late Devonian the Canning Basin slowly subsided, leaving much of the Fitzroy Trough as a near-shore shelf (the Lennard Shelf) some 300 km in length and several km wide. Both fringing and atoll stromatoporoid and algal reefs grew upon this shelf, with typical reef development including reef, back-reef, fore-reef and inter-reef facies. The Gogo Formation is inter-reef and composed of shales and siltstones with thin bands of limestone and numerous calcareous concretions. About half of the calcareous siltstone concretions contain fossils, chiefly phyllocarid crustaceans and fishes (Gardiner & Miles 1975). The formation is well dated on palaeontological grounds as Frasnian 1 α - to 1 β (Roberts *et al.* 1972; with references). Since Devonian times weathering has removed much of the softer inter-reef deposits of the Fitzroy Trough, leaving the fossil-bearing concretions lying on the surface. A map of the Gogo Formation localities is given by Miles (1971b: fig. 1). A few specimens were collected on an earlier expedition by H. A. Toombs of the British Museum (Natural History) in 1963.

The fishes have been prepared by the standard acetic acid techniques and one specimen (*Mimia*) has been serially sectioned. The specimens are uncrushed and often almost complete, which suggests that the concretions themselves developed during an early stage of diagenesis in still-water conditions.

The second aim of this paper is to discuss certain aspects of actinopterygian comparative morphology that may have a bearing on the problems of actinopterygian relationships and interrelationships. Thus the anatomical descriptions are divided into several parts each of which is followed by a discussion section. The discussions are intended to establish or propose primitive conditions in various groups (i.e. synapomorphies of those groups). Wherever possible homologies are established by congruence with other characters, but in some cases the criterion of commonality is used. I have also employed ontogenetic precedence and outgroup comparison as well as the stratigraphical succession in helping to establish the polarity of transformation series.

The term 'palaeoniscid' is used throughout for those fossil fishes which have traditionally been included within the extinct Palaeonisciformes. 'Actinopterygian' is used for any member of the group Actinopterygii, 'actinopteran' for members of the Actinopteri (Rosen *et al.* 1981) and 'osteichthyan' for bony fishes plus tetrapods. 'Sarcopterygian' refers to members of the Actinistia plus Choanata, while the term 'rhpidistian' is used for Osteolepiformes, Porolepiformes and Youngolepididae.

Specimen numbers are prefixed as follows: BMNH, British Museum (Natural History); RSM, Royal Scottish Museum; GSM, Institute of Geological Sciences, London.

Lettering used in text figures

aasc	anterior ampullary chamber	bpopc	branch of preopercular sensory canal
acv	foramen of anterior cerebral vein	bpt	basipterygoid process
aesc	external ampullary chamber	br	bridge of bone separating V and VII hyomandibular
af	area of fusion between occipital arch and otic capsule	Bsp	basisphenoid
a.ghy	area of attachment of geniohyoideus muscle	can	canal through propterygium
ahy	groove for afferent hyoidean artery	can.W	ascending canals of Williamson
aip 1	articular facet for first infrapharyngobranchial	Cb	ceratobranchial
alig	area of origin of aortic ligament	cao	aortic canal
amyd	dorsal anterior myodome	cdic	capsule housing diencephalon
amyv	ventral anterior myodome	Ch	ceratohyal
An	angular	chy	hyomandibular canal
ano	anterior nasal opening (external incurrent nostril)	cl	canal for lateral aorta
anpl	angular pit-line	Clav	clavicle
ap	anterior pit-line	CIm	cleithrum
apal	articular facet for autopalatine (palate)	cnc	cavity occupied by nasal capsule
apr	anterior process	copl	capsule housing optic lobes
apsc	posterior ampullary chamber	Cor	coronoid
Ar	articular	cor	canal from orbit to skull roof
art.H	articulation surface for hypohyal	corf	coracoid foramen
art.Hb	articulation surface for hypobranchial	cotel	canal joining orbit with telencephalon
ascf	anterior scapular foramen	crd	canal for ascending branch of superficial ophthalmic nerves
asp	ascending process of parasphenoid	csim	cavum sinus imparis
asup 1	articular surface for first suprpharyngobranchial	c.sp.	cell spaces
Aup	autopalatine	ctel	capsule housing telencephalon
Av	accessory vomerine tooth plate	dasc	dorsal opening of anterior semicircular canal
Bb	basibranchial	De	dentary
bhc	bucco-hypophysial canal	dend	tube or foramen for endolymphatic duct
bhm	foramen for branches of mandibular nerve to pit organs	Dhy	dermohyal
binc	tube or foramen for dorsal branch of infraorbital sensory canal in premaxilla; or pore opening therefrom	Dmpt	dermometapterygoid
		dop	depression for opercular cartilage?
		Dpl	dermopalatine
		dpl	dentary pit-line
		dpsc	dorsal opening of posterior semicircular canal
		Dspo	dermosphenotic
		dt	dentinal tubules

Eb	epibranchial	foa	foramen of orbital artery
Ecpt	ectopterygoid	foca	foramen of occipital artery
Enpt	entopterygoid	focn	foramen or notch for occipital nerve
ep	epural		
epl	epineural process	fona	foramen of orbitonasal artery
epopc	entrance of preopercular sensory canal	fopa	foramen for ophthalmic artery
		for	fenestrae linking dorsal myodomes
ethc	ethmoidal commissural sensory canal or pit opening therefrom	fos	otico-sphenoid fissure
		fotc	otico-occipital fissure
Exsc	extrascapular	fo _{tn} ₁	foramen of otic nerve
Exsc ₁	medial extrascapular	fpal	foramen of palatine branch of facial nerve
Exsc ₂	lateral extrascapular		
		fpal ₂	entry foramen of palatine nerve into parabasal or palatine canal
fapcv	foramen for anterior tributary of posterior cerebral vein		
fbmand.ext. VII	foramen for branches of external mandibular branch of facial nerve	Fr	frontal
		frd	foramen or notch for ascending branch of superficial ophthalmic nerves
fboca	foramen for branch of occipital artery	frla	foramen of ramus lateralis accessorius
fb. IX	foramen for branches of glossopharyngeal nerve to pit-line	frla ₁ , frla ₂	foramen of branch of ramus lateralis accessorius
fb. X	foramen for branches of vagus nerve to pit-line	frmx	foramen for maxillary branch of trigeminal nerve
fc	ceratobranchial foramen	fst. IX	foramen of supratemporal branch of glossopharyngeal nerve
fendc	fenestra endonarina communis		
fepsa	foramen for efferent pseudobranchial artery	fv	ventral otic fissure
fexna	fenestra exonarina anterior	fvii	venous foramen
ffr	fringing fulcra		
fhm	hyomandibular facet		
fhm. VII	foramen of hyomandibular trunk of facial nerve	g	ganoine
		gI	gap in ossification of wall of olfactory nerve canal
fhm. VII + pal	foramen of hyomandibular and palatine trunks of facial nerve	gboca	groove for branch of occipital artery
fhy. VII	foramen for hyoid branch of facial nerve	gdend	groove for endolymphatic duct
fia	foramen for intersegmental artery	gf	glenoid fossa
fica	foramen of internal carotid artery	ghm. VII	groove for hyomandibular trunk of facial nerve
fica ₂	ascending canal of internal carotid artery in basisphenoid pedicel	gic	groove for internal carotid artery
		GI	lateral gular
fi. Sh	canals for fibres of Sharpey	gla	groove for lateral aorta
fm	foramen magnum	Gm	median gular
fmand. V	foramen for mandibular branch of trigeminal nerve	gmand.ext. VII	groove for external mandibular branch of facial nerve
fmand. VII	foramen for mandibular branch of facial nerve	goa	groove for orbital artery
		goca	groove for occipital artery
fmand.int. VII	foramen for internal mandibular branch of facial nerve	gona	groove for orbitonasal artery
		gpl	gular pit-line
		gpcv	groove for posterior cerebral vein
fm _{xv} . V buc. VII	foramen for maxillary branch of trigeminal and buccal branch of facial nerve	gph. X	groove or foramen for pharyngeal branch of vagus nerve

gr	groove in dermopalatines and ectopterygoid and in coronoids and prearticular	Mpt mr msc mscp mtp mvfon Mx	metapterygoid marginal fin-ray mesocoracoid arch mesocoracoid process metapterygium margin of vestibular fontanelle maxilla
gst.IX	groove for supratemporal branch of glossopharyngeal nerve		
gst.X	groove for supratemporal branch of vagus nerve		
g.X	groove for vagus nerve	n	notch in margin of supratemporal
h ₁	first hypural	Na	nasal
ha	haemal arch	na	neural arch
Hb	hypobranchial	nabc	foramen of nasobasal canal in floor of nasal capsule
hbpt	hole for basiptyergoid process		
hc	haemal canal	nc	nasal capsule
Hh	hypohyal	nfencd	notch for posterolateral part of fenestra endonarina communis
hll	horizontal longitudinal lamina		
hpl	horizontal pit-line		
Hy	hyomandibula	nona not npl	notch for orbitonasal artery notochordal canal nasal pit-line
Iclav	interclavicle		
iepl	insertion points of ethmopalatine ligament	oahm	area of origin of adductor hyomandibulae portion of dorsal constrictor
Ih	interhyal		
inc	tube or foramen for infraorbital sensory canal or pore opening therefrom	oaop	area of origin of adductor opercularis portion of dorsal constrictor
inw	internasal wall		
ios	interorbital septum	oatm	area of origin of anterior trunk muscles
Ip	infrapharyngobranchial		
It	intertemporal	oem	area of origin of eye muscles
ivl	area of insertion of intervertebral ligament	oexr	area of origin of external rectus muscle
jc	jugular canal	oims ₁	area of origin of first intermuscular septum
jg	jugular groove	oims ₂	area of origin of second intermuscular septum
Ju	jugal	olab	area of origin of levator branchialis muscles
Lac	lachrymal		
lapf	fossa for levator arcus palatini muscle	olap	area of origin of levator palatini muscle
lc	cephalic division of lateral line	Op	opercular
lcc	lateral cranial canal	orb	orbit
lcom	lateral commissure	orc	orbito-rostral canal
ll	foramen through which lateral line enters supratemporal or lateral line scale	Ors osubc	orbitosphenoid area of origin of subcephalic muscle
lmc	lower muscle canal (= supracoracoid foramen)	p	pores in premaxilla, nasal and lachrymal
lmpt	lamina of metapterygoid		
lnabc	lateral nasobasal canal	Pa pamp Par parc	parietal parampullary process prearticular opening or course of parabasal canal
Men	mentomeckelian		
mc	mandibular sensory canal		
mcv	foramen of middle cerebral vein	pchl	pit for ceratohyal ligament
Mk	ossified Meckelian cartilage	Pcl	postcleithrum
mnabc	medial nasobasal canal	pdf	posterior dorsal fontanelle
mp	middle pit-line	ped	'alisphenoid pedicel'

pesc	posterior opening of external semicircular canal	rmet rmye	recess housing metencephalon recess housing myelencephalon
Pg	pelvic girdle		
pinf	pineal foramen	Ro	rostral
pitf	pituitary fossa	ropl	recess housing optic lobe
plcc	posterior opening of lateral cranial canal	rot rpl	otic nerve radial plate
Pmx	premaxilla	rsoc	recess on roof of otic region
pno	posterior nasal opening (external excurrent nostril)	rtel	recess housing telencephalon
pnw	postnasal wall		
Po	postorbital	sacr	saccular recess
po	lateral line pore	San	supra-angular
podp	pharyngeal (parotic) tooth plate	sc scf	scale scapular or coracoid foramen
Pop	preopercular	Scl	supracleithrum
popc	preopercular sensory canal	sgf	supraglenoid foramen
por	postorbital process	sn	supraneural
Pp	postparietal	Soc	supraoccipital
pp	posterior pit-line	Sop	subopercular
prepf	prepalatine floor	Sp	suprapharyngobranchial
prh	hyoid process of branchiostegal	sp spic	spiracular opening spiracular bar
Pro	prootic	spig	spiracular groove
prob	prootic bridge (dorsum sellae)	spip	spiracular tooth plate
prof	foramen or canal for profundus nerve	ssu	division of labyrinth cavity for the sinus superior
prof ₂	foramen or canal for branches of profundus nerve	St stc	supratemporal supratemporal commissural sensory canal
propt	propterygium		
Prscl	presupracleithrum	suc	tube or foramen for supraorbital sensory canal or pore opening therefrom
psc	cavity occupied by, or ridge over, posterior semicircular canal	svfotc	sub-vagal portion of otico-occipital fissure
Psp	parasphenoid		
Pt	post-temporal	svr	recess housing saccus vasculosus
Pts	pterosphenoid		
pu8	eighth pre-ural centrum		
pv	foramen or pathway for pituitary vein	Tab tp	tabular toothplate
Qu	quadrate	utr	utricular recess
Quj	quadratojugal		
qujpl	quadratojugal pit-line	va vfon vnabc vnabcf	ventral arch vestibular fontanelle ventral nasobasal canal opening of ventral nasobasal canal in roof of mouth
r	radial	Vo	vomer
rbuc	buccal nerve	vpl	vertical pit-line
Rbr	branchiostegal ray		
rcor	coracoid ridge		
rdo	ascending branches of superficial ophthalmic nerves	Z	zygal plate
rhm + pal	hyomandibular trunk and palatine branch of facial nerve		
rla	ramus lateralis accessorius	I	tube or foramen for olfactory tracts

II	optic fenestra	VI ₁ , VI ₂	foramina of abducens nerve
III	notch, foramen or canal of oculomotor nerve	VII	foramen or canal for facial nerve
IV	notch or foramen of trochlear nerve	VII.lat	foramen or canal for lateralis trunk of facial nerve
V	foramen or canal for trigeminal nerve	IX	foramen of glossopharyngeal nerve
VI	foramen of abducens nerve	X	foramen of vagus nerve

Systematic descriptions

Family **STEGOTRACHELIDAE** Gardiner, 1963

Genus **MIMIA** Gardiner & Bartram, 1977

DIAGNOSIS. Stem-group actinopteran fishes in which the ventral otic fissure passes into the rear of the orbit; the parasphenoid is broad but without basiptyergoid or ascending processes; the otico-sphenoid fissure is cartilage-filled; a pair of orbitonasal arteries passed into the orbit immediately lateral to the ventral otic fissure; the spiracular groove is wide, there is a spiracular slit between intertemporal and dermosphenotic; the neurocranium contains a lateral cranial canal; the perforated pectoral propterygium is embraced by the bases of the marginal rays; and basal and fringing fulcra are present.

TYPE SPECIES. *Mimia toombsi* Gardiner & Bartram, 1977.

REMARKS. *Mimia* and *Moythomasia* are closely related Devonian fishes which have been placed in the family Stegotrachelidae (Gardiner 1963; Gardiner & Bartram 1977). Unfortunately all the characters they share with *Stegotrachelus* are primitive, but until we know more of the internal anatomy of *Stegotrachelus* and other stem-group actinopterans it is premature to suggest alternative family groupings. Consequently the genera will be referred to either as *Mimia* and *Moythomasia* or as 'the Gogo palaeoniscids' in the following account.

Mimia toombsi Gardiner & Bartram, 1977

- 1970 Devonian stegotrachelid; Gardiner: 285; fig. 3.
- 1971 Stegotrachelid palaeoniscoid; Gardiner *in* Moy-Thomas & Miles: figs 5, 6.
- 1973 Gogo palaeoniscid 'A'; Gardiner: 106; figs 1, 2, 6, 8, 9.
- 1973 Gogo palaeoniscid 'B'; Gardiner: figs 3, 4.
- 1975 Gogo palaeoniscid; Gardiner & Miles: fig. 2.
- 1977b Palaeoniscoid; Patterson: fig. 1B.
- 1977 *Mimia toombsi* Gardiner & Bartram: 228; figs 1-6.

DIAGNOSIS. As for genus.

HOLOTYPE. Western Australian Museum 70.4.245; partly disarticulated specimen wanting fins, in counterpart, from the Upper Devonian, Gogo Shales, Gogo Station (H.A.T. 67/80, see Miles 1971b), Fitzroy Crossing, W. Australia.

SPECIMENS. This study is based on 61 specimens from the following Gogo localities: 21, 25, 27, 30, 36, 37, 42, 47, 54, 55, 56, 63, 73, 80, 84, 87, 89, 91, 92, 302 (for Gogo localities see Miles 1971b: fig. 1).

Genus **MOYTHOMASIA** Gross, 1950

[= *Aldingeria* Gross 1942:431]

DIAGNOSIS. See Gross (1942: 430) and Jessen (1968: 89). In addition the ventral otic fissure passes into the rear of the orbit; the parasphenoid is broad with a rudimentary ascending process but no basiptyergoid process; the palatoquadrate has a short anterior process; there is a spiracular slit between the intertemporal and dermosphenotic and the dermosphenotic is hinged

to the jugal as in *Mimia* and *Cheirolepis*; the neurocranium has a lateral cranial canal; the lower jaw has a supra-angular; the pectoral fin has a perforated propterygium embraced by the bases of the marginal rays; there are prominent basal fulcra above and below tail; and fringing fulcra are present on all fins.

TYPE SPECIES. *Moythomasia perforata* (Gross).

REMARKS. The genus is known from the Devonian (Frasnian) of Kokenhusen, Latvia, Bergisch Gladbach and Wildungen, Germany and Gogo, Western Australia (Gross 1950, 1953; Jessen 1968; Gardiner & Miles 1975; Gardiner & Bartram 1977).

Moythomasia durgaringa Gardiner & Bartram, 1977

1973 Gogo palaeoniscid 'B'; Gardiner: figs 5 and 7 only (not figs 3, 4).

1977 *Moythomasia durgaringa* Gardiner & Bartram: 238; fig. 7.

1981 *Moythomasia durgaringia* Gardiner & Bartram; Forey & Gardiner: 140.

DIAGNOSIS (emended). A *Moythomasia* with scales with up to 15 serrations posteriorly.

HOLOTYPE. Western Australian Museum, 70.4.244; partly disarticulated head and body in counterpart from the Upper Devonian, Gogo Shales, Gogo Station (H.A.T. 67, see Miles 1971b), Fitzroy Crossing, W. Australia.

SPECIMENS. This study is based on 18 specimens from the following Gogo localities: 36, 37, 72, 78, 80, 84, 86, 89.

Neurocranium: general features

The neurocrania of *Mimia* and *Moythomasia* are very similar, more or less completely ossified, with both external and posterior semicircular canals visible externally.

Comparative measurements show that in both the maximum breadth (between the postorbital processes) is about 60% of the total length, while the depth, which remains remarkably constant throughout, is some 34% of the length. The orbital length (postorbital process to tip of ethmoid) constitutes at least 55% of total braincase length in *Mimia*, but in *Moythomasia* the orbital length is 50% of total braincase length.

Although the neurocrania are, for the most part, both perichondrally and endochondrally ossified, the degree of ossification is greater posteriorly. Thus the greatest thickness of endochondral bone occurs around the tip of the notochord (in the area of the prootic bridge) and there is little endochondral bone in front of the basipterygoid process ventrally or the pineal foramen dorsally. Well-developed endochondral bone is confined to the postorbital portion of the braincase and that area around the hypophyseal foramen (including the basipterygoid process). In this respect it is interesting to note that ossification of the osteichthyan skull commences around the notochordal plate and proceeds anteriorly. The whole of the preorbital regions of the neurocrania of *Mimia* and *Moythomasia* are only perichondrally ossified, while in front of the basipterygoid processes up to the anterior limits of the orbits endochondral bone can only be recognized in thin section as mere wisps of tissue in the more lateral areas of the neurocranial ossifications. In presumed younger individuals the area anterior to the nasal capsules is often not even perichondrally ossified; only in a few mature individuals does a complete layer of perichondral bone occur.

The anterior region of the neurocrania of *Mimia* and *Moythomasia* is thus only perichondrally ossified. In this respect they resemble some of the pholidophorid and leptolepid neurocrania described by Patterson (1975: 473), of which he remarked 'the ethmoid region is often missing from the fossils, and when preserved is as a rule less thoroughly ossified'; he added that the ethmoid area is frequently only perichondrally ossified. Although the ethmoid region is as a rule less thoroughly ossified in primitive actinopterygians (cf. *Pteronisculus* Nielsen 1942, *Birgeria* Nielsen 1949, *Kansasiella* Poplin 1974), in the majority of other fossil osteichthyans this region is invariably endochondrally ossified (*Nesides* Stensjö 1932b, *Eusthenopteron* Jarvik 1954, *Glyptolepis* Jarvik 1972, *Chirodipterus* Säve-Söderbergh 1952, *Griphognathus* Miles 1977).

From what evidence is available it appears that the neurocranium of chondrichthyans, acanthodians and placoderms is composed solely of perichondral bone. If the Actinopterygii are the sister-group of the Sarcopterygii (Rosen *et al.* 1981) then the absence of endochondral bone in the snout of early actinopterygians is probably a primitive feature.

The endochondral bone, where it occurs in the neurocrania of *Mimia* and *Moythomasia*, is thick and cancellate with large medullary spaces surrounded by delicate laminae, and with external and internal surfaces and all canals for vessels or nerves lined with thin, laminate, perichondral bone which shows few traces of radial structures; consequently it is difficult to deduce individual ossification centres. In this they resemble many fossil actinopterygians including palaeoniscids, perleidids, pholidopleurids, parasemionotids (Nielsen 1942, 1949) and pholidophorids (Patterson 1975: 288).

While separate ossifications are not evident in the neurocrania of many primitive actinopterygians, there are several notable exceptions. Discrete ossifications have been described in the palaeoniscids *Cosmoptychius* (Watson 1928: 49), *Pteronisculus magnus* (Nielsen 1942) and *Birgeria* (Stensiö 1921, Nielsen 1949), in *Perleidus* cf. *stoschiensis* (Patterson 1975: 456), and in the living *Polypterus*, *Acipenser* and *Polyodon* (see Patterson 1975: 463 for summary). Elsewhere within the actinopterygians ossification centres are also recognizable in parasemionotids (Lehman 1952: 162, Patterson 1975: 432), caturids such as '*Aspidorhynchus*' (Rayner 1948: 315, Patterson 1975: 436), *Macrepistius* (Schaeffer 1971) and *Caturus furcatus* (Patterson 1975: 441), and in the amiids *Enneles* (Santos 1960), *Sinamia* (Stensiö 1935) and the extant *Amia*. They have also been described in the semionotids *Lepidotes* (Woodward 1916, Patterson 1975: 449) and the living *Lepisosteus*, in the pachycormids *Pachycormus* (Rayner 1948, Patterson 1975: 443), *Hypsocormus* (Stensiö 1935) and *Protosphyraena* (Loomis 1900, Lehman 1949), in the Mesozoic pholidophorids and leptolepids (Patterson 1975) and in most Recent teleosts.

In all the specimens of *Mimia* and *Moythomasia* examined the braincase was fully ossified and sutureless, yet some specimens of *Moythomasia* are only a third the size of others. Patterson (1975: 287) observed a similar size discrepancy in the ossified neurocrania of *Pholidophorus bechei*, so presumably as in *Pholidophorus* ossification in *Mimia* and *Moythomasia* must have set in early in ontogeny and growth have been terminated by fusion of the bones.

However, the absence of separate ossifications in the neurocrania of Devonian actinopterygians and most of the known primitive fossil actinopterygians, and the presence of separate bones in later actinopterygians, can be accounted for by two hypotheses. The neurocranium may have ossified primitively in a single piece and in subsequent evolution have fragmented into several ossification centres, independently in different lines (Stensiö 1932b: 297). Alternatively the neurocranium may always have ossified from a discrete set of centres, in more primitive forms growth being thus terminated by fusion of the constituent bones, whereas in others the sutures remained open to allow persistent growth, as in living teleosts (Gardiner 1960: 359, Schaeffer 1971: 21, Patterson 1975: 288). Elsewhere discrete endocranial bones are found in *Acanthodes* (Miles 1971a), *Ctenurella* (Miles & Young 1977), all post-Devonian actinistians (and possibly even *Nesides* in which the back of the skull is missing), *Eusthenopteron* (Stensiö 1932b: 297, Jarvik 1972) and tetrapods. Separate bones have also been described in the Devonian dipnoan *Dipnorhynchus* (Campbell & Barwick 1982), but with the exception of the exoccipitals of *Neoceratodus* no separate ossifications have ever been noted in Recent dipnoan neurocrania. In shark neurocrania perichondral bone develops at the surface of the individual tesserae (Kemp & Westrin 1979) and there are therefore numerous ossification centres.

If the phylogenetic fragmentation hypothesis is correct then fragmentation must have occurred on at least five separate occasions: within the chondrichthyans, within the acanthodians, within the placoderms, within the actinopterygians and once again within the remaining osteichthyans. This hypothesis is thus extravagant, and since the endochondral bone of the braincase in all Recent gnathostomes grows from a suite of fixed centres it is difficult to believe that in the braincase of Devonian fishes endochondral (and perichondral for that matter) bone grew in some as yet undescribed fashion. Consequently, I am forced to continue to support

the non-fragmentation hypothesis of braincase ossification, in which it is proposed that the neurocranium always ossified from a discrete set of centres.

Unfortunately, this hypothesis has been further complicated in actinopterygians by two additional, conflicting hypotheses, either that there has been an increase of ossification centres ('fragmentation'), or that there has been an decrease ('fusion', loss). But, as Patterson (1975: 470) points out, most of the evidence in support of a subdivided neurocranium being the derived condition rests on the assumption that teleosts possess the most highly subdivided neurocrania. Patterson (1975: 470) has however clearly demonstrated that the braincase of living teleosts contains fewer endochondral bones than the more primitive pholidophorids, and they certainly contain fewer bones than early pachycormids (personal observation). From his survey of braincases Patterson (1975) has shown that 'the dominant process in actinopterygian evolution has been reduction in the number of endocranial ossifications, not increase . . . examples of loss being numerous especially in the pholidophorids and teleosts'.

Other evidence for the fragmentation hypothesis rests on the observations that in *Polypterus* and in palaeoniscids, where ossification patterns are known (*Cosmoptychius* and *Birgeria*), there are fewer bones than in teleosts and many halecomorphs, while the Permian *Acanthodes* has a pattern of neurocranial bones similar to *Cosmoptychius*. Patterson (1975: 465) has demonstrated that the conditions in *Polypterus* and *Birgeria* are similar and that they both differ considerably from the palaeoniscid type from which they can most reasonably be derived by assuming loss of ossifications.

Cosmoptychius (Watson 1928, Schaeffer 1971) on the other hand is known from but a single, incomplete specimen. It is similar in many respects to some of the smaller skulls of *Moythomasia* and, as Patterson (1975: 402) commented, is probably composed of the same series of bones as in most palaeoniscids. The fact that there is but one large paired ossification, one small median ossification and two pairs of smaller ossifications in this specimen is not evidence that the braincase ossified from the same number of centres. Thus, the occipital ossification probably included basi- and exoccipitals as well as an intercalar, and the upper part of the occiput, which is missing from the specimen, must have included epioccipitals.

Finally the pattern of ossification in *Acanthodes* is superficially actinopterygian-like and said to resemble that in *Cosmoptychius* (Schaeffer 1971, Miles 1973a). But the braincase of *Acanthodes* (Miles 1971a: fig. 4.7) differs from most actinopterygians in not possessing either epioccipitals or prootics and in not having endochondral ossification. It is also possible (Denison 1979) that the condition in *Acanthodes* (the last of the acanthodians) is not primitive for acanthodians and that *Acanthodes*, like the living chondrosteans and *Polypterus*, may have lost several ossification centres.

The conclusion which may be drawn from this discussion is that the hypothesis of loss of neurocranial ossification centres has more to support it than the conflicting hypothesis of increase of centres by fragmentation. It follows from the acceptance of this conclusion that the common ancestor of the gnathostomes possessed a neurocranium which ossified from a number of centres and that the number of centres in chondrichthyans is far greater than in the rest of the gnathostomes. Furthermore the pattern of ossification seen in chondrichthyans is different from that in other gnathostomes. In chondrichthyans the prismatic calcifications remain tesserate throughout life and the cap zone of the individual tesserae forms a thin veneer of perichondral bone; growth is accomplished by enlargement of the individual prisms (Kemp & Westrin 1979). In osteichthyans the ossification centres are far fewer, ossification commences as a disc on the surface of the cartilage model and the sutures may remain open so that growth is continuous.

Within the various non-chondrichthyan lineages loss of neurocranial ossification centres has occurred independently, maybe in relation to varying mechanical factors such as neurokinesis etc., and until the phylogenetic homologies have been worked out for each group we can only presume that topographically similar bones in the neurocrania of acanthodians, actinopterygians, actinistians, rhipidistians and tetrapods are not necessarily homologous.

Miles (1977) has recently argued that the presence of endochondral bone in the snout of the Devonian dipnoan *Griphognathus* is primitive in relation to the condition in other Devonian dipnoans such as *Chirodipterus* and *Holodipterus*, where endochondral bone is restricted to the

otic and occipital regions. But if, as argued above, endochondral bone is primitively absent from the snout of actinopterygians, and the actinopterygians are the sister-group of the remaining osteichthyans (Gardiner 1973, Rosen *et al.* 1981), then it is more likely that the condition of the snout of *Griphognathus* is specialized in respect to *Chirodipterus* and *Holodipterus*.

In order to substantiate the argument that endochondral bone is primitively absent from the snout of actinopterygians it is necessary to re-examine the occurrence of endochondral bone in early vertebrates.

Some authors (Miles 1977, Schaeffer 1971) consider perichondral and endochondral bone to be of equal antiquity and also primitive for all bony vertebrates. There is little doubt that perichondral bone, like dermal bone, is a primitive vertebrate tissue since both occur in cephalaspids (Stensiö 1927, 1932a), placoderms (Stensiö 1963a, b), acanthodians, bony fishes and tetrapods. On the other hand endochondral bone has a more limited distribution. In the whole of the Agnatha the only record of endochondral bone is in the cephalaspid *Boreaspis* (Wängsjö 1952: fig. 1). Re-examination of Wängsjö's thin section of *Boreaspis* has convinced me that this is merely an extensive perichondral ossification similar to that seen in thin sections of other cephalaspids. It is worth noting that in mammals growth of a perichondral ossification may result in replacement of the entire cartilage that it envelops, and that in very weakly ossified neurocrania, such as that of the chondrosteian *Polyodon*, the bones consist merely of scale-like perichondral ossifications.

Through the kindness of Dr G. Young I have had the opportunity of examining several neurocrania of Devonian placoderms from Australia including *Brindabellaspis stensioi* Young, *Buchanosteus confertituberculatus* (Chapman) and *Wijdeaspis warrooensis* Young; all show extensive perichondral ossifications but none shows any trace of endochondral bone. Recently Miles & Young (1977: 168; fig. 21) have stated that in one specimen of the ptyctodontid *Ctenurella gardineri* Miles & Young endochondral bone is present in the ethmoidal bone. Re-examination of this specimen (BMNH P.57665) convinces me that what they termed endochondral bone is probably calcified cartilage. If placoderms lack endochondral bone and are more closely related to chondrichthyans than to other gnathostomes (Miles & Young 1977), or are the sister-group of osteichthyans, then endochondral bone must be considered a specialization of osteichthyans, as Rosen *et al.* (1981) presumed, and the absence of endochondral bone from the snout of Devonian actinopterygians and dipnoans is a primitive character.

Occipital region

The neurocrania of *Mimia* and *Moythomasia* are ossified in a single piece as in the palaeoniscids *Boreosomus* (Nielsen 1942), *Pteronisculus macropterus* (Beltan 1968) and *Kansasiella* (Poplin 1974); consequently individual bones are not apparent and it is not easy to delimit regions, except in a very general way. Here the occipital region is taken to be that area of braincase behind the occipital fissure (fissura otico-occipitalis) and below the vestibular fontanelle and extending anteriorly as far as the ventral otic fissure (fissura oticalis ventralis).

Mimia toombsi

Dorsally the occipital region is separated from the otic by a small, oval posterior dorsal fontanelle (Pl. 1; pdf, Figs 26, 79). This represents the expanded dorsal portion of the occipital fissure. The posterior dorsal fontanelle is smaller than that in *Kansasiella* (Poplin 1974: fig. 12), *Pteronisculus* (Nielsen 1942: fig. 7), *Australosomus* (Nielsen 1949: fig. 3) and *Kentuckia* (Rayner 1951: fig. 6), and is lined throughout with perichondral bone. Although this fontanelle is also perichondrally lined in *Australosomus* (Nielsen 1949: 27) there is no perichondral lining in *Pteronisculus* (Nielsen 1942: 41) and presumably it was cartilage-filled. The fontanelle is closed by bone in some specimens of *Boreosomus* whereas in others it remains open (Nielsen 1942: 287).

The occipital fissure (fotc, Figs 4, 5, 6, 12, 13, 15, 50), which represents the persistent metotic fissure between the occipital arch and otic capsule of the embryo, passes anteroventrally from

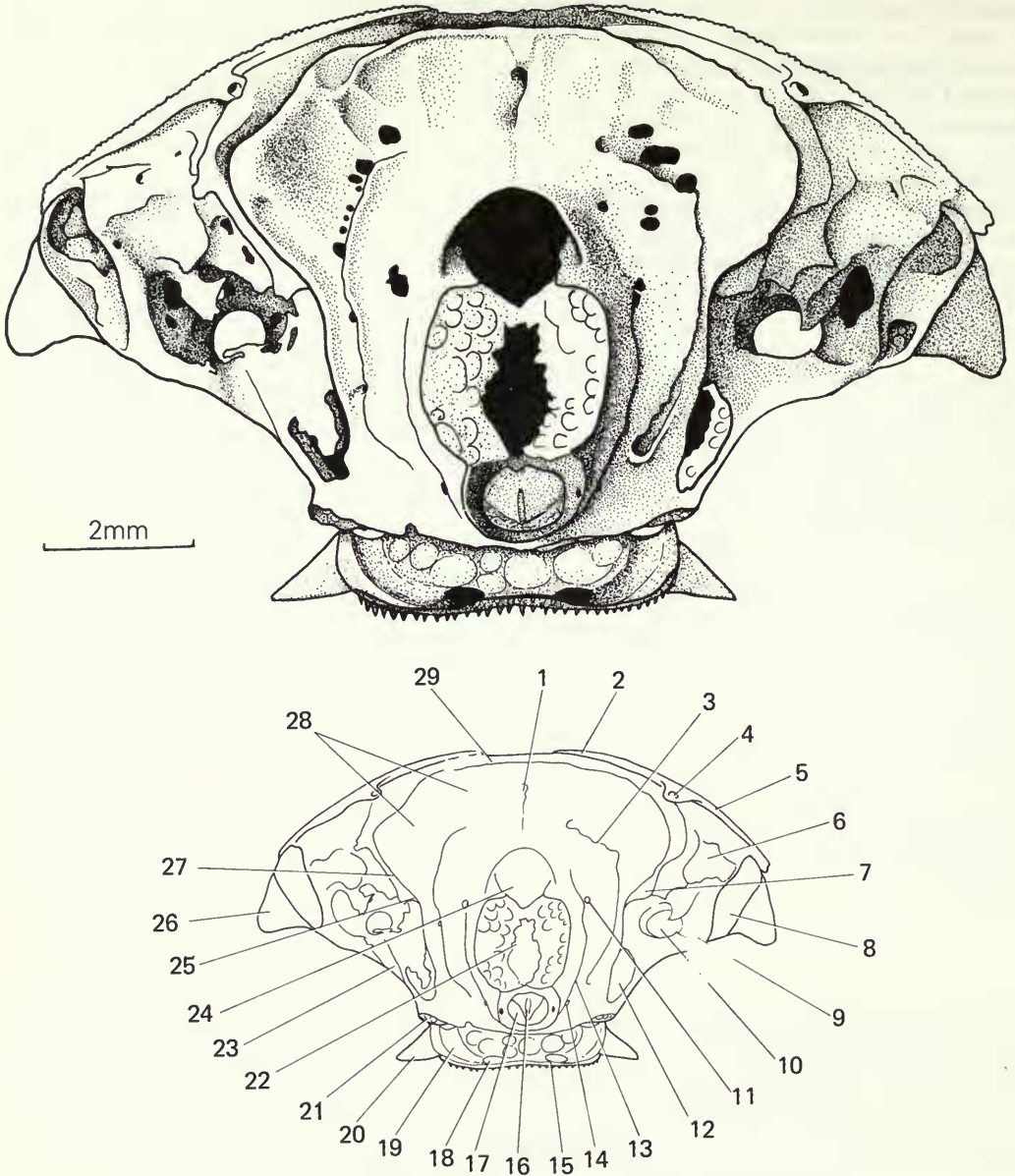


Fig. 1 *Mimia toombsi* Gardiner & Bartram. Neurocranium and attached dermal bones in posterior view, basisphenoid displaced ventrally; from BMNH P.56504. Key (diagram below): 1, ivl; 2, Pa; 3, oims₁; 4, ll; 5, St; 6, oahm + oaop; 7, apsc; 8, fhm; 9, ghm.VII; 10, jc; 11, focn; 12, vfon; 13, oims₂; 14, foca; 15, Psp; 16, alig; 17, cao; 18, fica; 19, gona; 20, bpt; 21, aip 1; 22, not 23, goa; 24, fm; 25, X; 26, por; 27, fotc; 28, oatm; 29, pdf. For explanation of lettering used on text-figures, see pp. 177–181.

the posterior dorsal fontanelle to terminate in an ovoid vestibular fontanelle. The vestibular fontanelle (vfon, Figs 1, 5, 13, 14, 15, 50) has no perichondral lining and was presumably cartilage-filled. It represents an area between adjacent ossifications (opisthotic, basioccipital and prootic ossifications deduced from Patterson 1975: 461) and is one of the few areas of the braincase which remains unossified in the adult early osteichthyan.

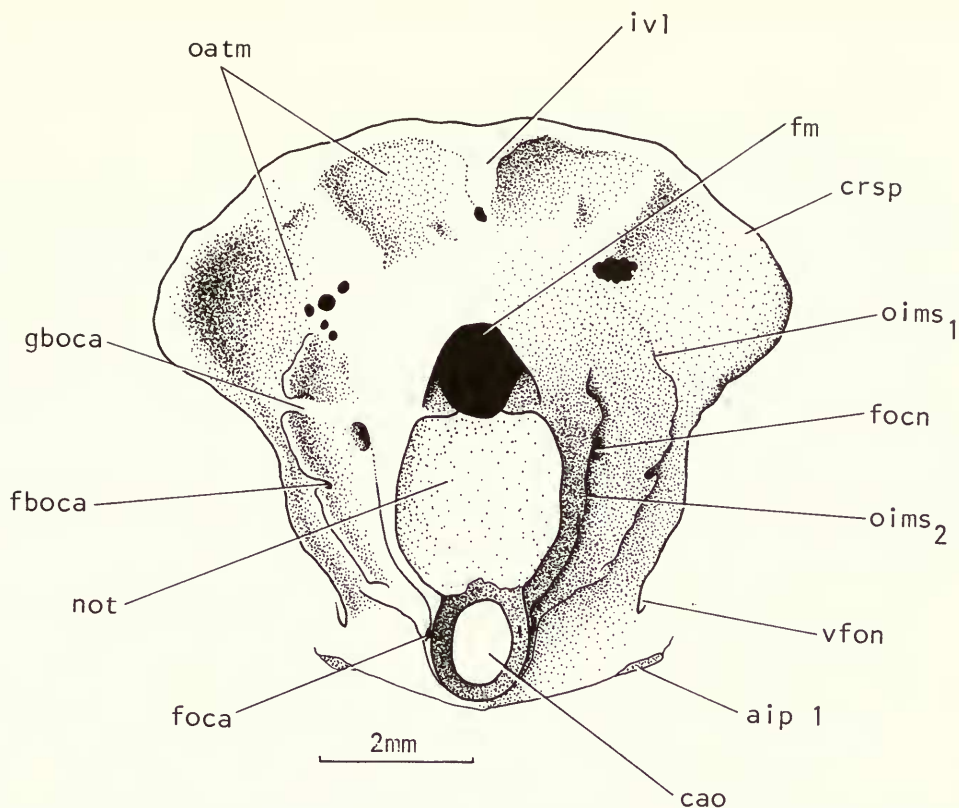


Fig. 2 *Mimia toombsi* Gardiner & Bartram. Occipital ossification in posterior view, from BMNH P.53243.

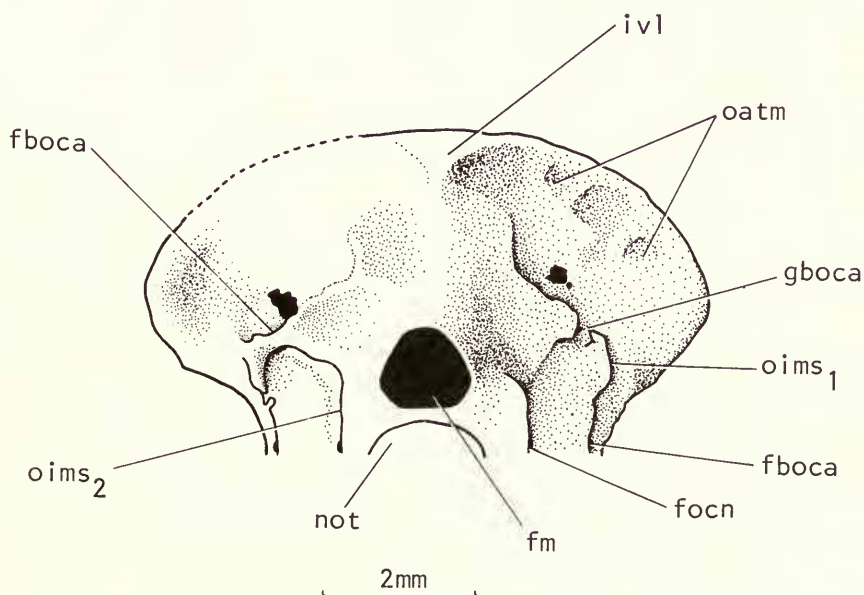


Fig. 3 *Mimia toombsi* Gardiner & Bartram. Dorsal part of the occipital ossification in posterior view, from BMNH P.56496.

The vestibular fontanelle of *Mimia* is somewhat smaller than in *Kansasiella* (Poplin 1974: fig. 13) and much smaller than in either *Kentuckia* (Rayner 1951: fig. 7) or *Pteronisculus* (Nielsen 1942: fig. 4). In size and shape it is quite similar to that in *Pholidophorus bechei* (Patterson 1975: fig. 56).

In early, less specialized, palaeoniscids the occipital fissure is complete and perichondrally lined throughout, except in *Moythomasia* (see p. 201 and Figs 8, 9), where a small area above the upper margins of the vagus canal lacks perichondral bone, and in some individuals of *Boreosomus piveteaui* (Nielsen 1942: fig. 59) where the mid-dorsal part of the fissure may be closed by a narrow bridge of bone. In other later, more advanced palaeoniscids such as *Birgeria* (Nielsen 1949: 190) the perichondral lining is missing and the fissure is presumably already cartilage-filled.

Anteriorly the occipital region in *Mimia* is bounded by another, completely separate fissure, the ventral otic fissure. This fissure (fv, Figs 13, 14, 15, 16, 22, 26, 50) lies in the floor of the neurocranium and passes up immediately behind the foramen for the pituitary vein and anterior to the foramen for the abducens nerve. The fissure is not perichondrally lined and was cartilage-filled in life; it represents the cartilage remaining between ossifications in the trabeculae (+ polar cartilages) and parachordals, and must represent the gap between the chordal and prechordal skeleton of the embryo. The fissure separates the basioccipital from the basisphenoid (ossifications deduced from Patterson, 1975) in the mid-line and from the prootics

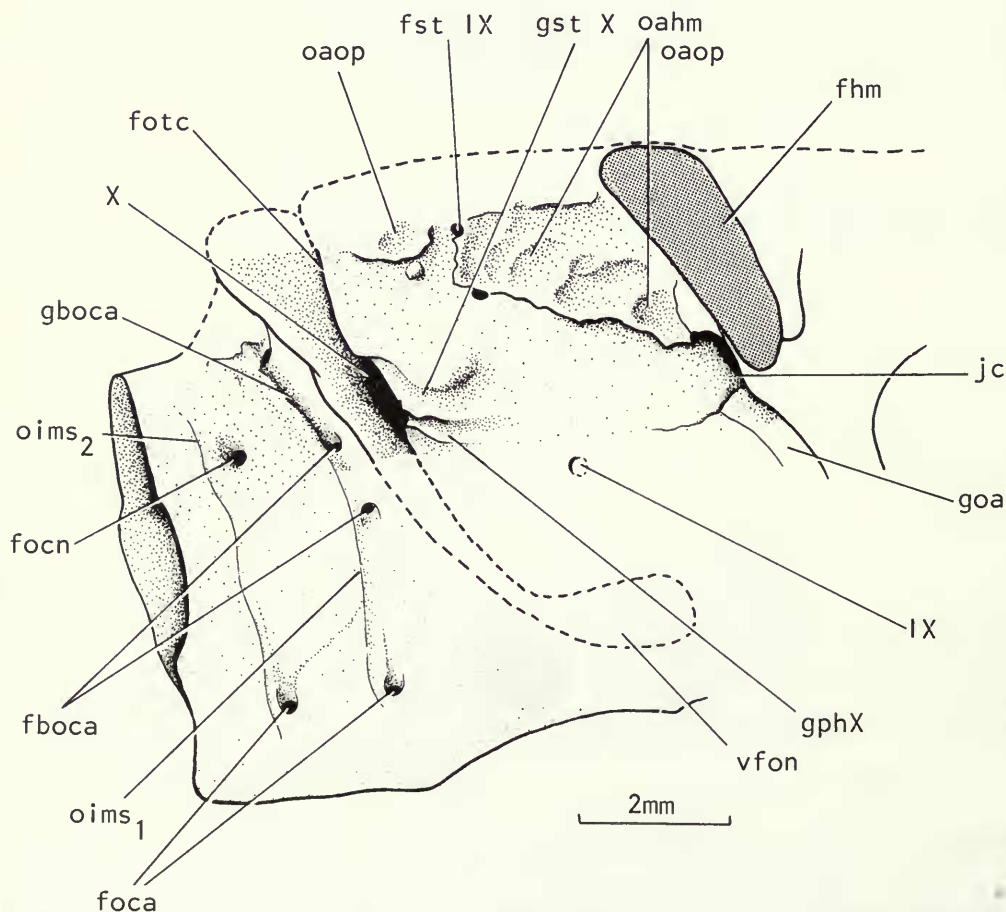


Fig. 4 *Mimia toombsi* Gardiner & Bartram. Otic and occipital regions in right lateral view, from BMNH P.56501.

dorsolaterally. From the floor of the neurocranium the fissure passes up behind the 'prootic' bridge to open into the front of the notochordal canal (not, Figs 25, 26). Laterally, at the level of the presumed junction between the basioccipital and prootics, the ventral otic fissure gives way on either side to a large foramen for the orbitonasal artery (fona, Figs 15, 50).

In the Gogo palaeoniscids the ventral otic fissure is therefore situated below the hind wall of the orbit and well in front of the vestibular fontanelle, from which it is separated by the bony wall of the neurocranium (the prootic and basioccipital). The ventral otic fissure is also separated from the vestibular fontanelle in other palaeoniscids such as *Kansasiella* (Poplin 1974: figs 13, 14), *Pteronisculus macropterus* (Beltan 1968: fig. 2) and *Boreosomus* (Nielsen 1942: fig. 63).

Although the limits of the individual ossifications making up the occipital region cannot be made out with certainty because in most cases individual sutures are absent, in some specimens and in certain areas ossification centres can be determined with considerable confidence. In all specimens of the Gogo palaeoniscids the floor and roof of the notochordal canal (and neurocranial floor) are incompletely ossified in the mid-line posteriorly, and in one specimen of *Mimia* (BMNH P.53250) there is a median suture running the whole length of the floor of the notochordal canal from the ventral otic fissure to the posterior limit of the neurocranium. This obviously paired ossification in the floor of the braincase must be the basioccipital. Elsewhere in osteichthyans (including tetrapods) the basioccipital is usually a median ossification (except perhaps for *Polypterus* and *Pachycormus*; Patterson 1975: 445, 448), but its origin must have been from paired ossification centres in the parachordal cartilages. Interestingly the basioccipital of *Acanthodes* (Miles 1973a: fig. 11) is incised in the mid-line both anteriorly and posteriorly and this is taken to indicate the paired origin of that perichondral bone. In front of the foramen magnum the basioccipital forms the floor of the neurocranium, the floor and lateral walls of the notochordal canal (see Fig. 25) and the ventral and posterior margins of the vestibular fontanelle. Anterolaterally the basioccipital passes indistinguishably into the prootics. The basioccipital fails to meet in the mid-line posteriorly beneath the notochordal canal in several other palaeoniscids, thus the notochordal canal is contiguous with the aortic canal in *Pteronisculus* (Nielsen 1942: 32), *Kansasiella* (Poplin 1974: figs 11, 20), *Boreosomus* (Nielsen 1942: fig. 61) and *Cosmoptychius* (Schaeffer 1971).

The roof of the notochordal canal and the floor of the foramen magnum is made up by another pair of ossifications, the exoccipitals. This can be recognized because the ossification centres for these bones in other osteichthyans lie lateral and somewhat ventral to the floor of the foramen magnum, and because, although the foramen magnum is completely lined with bone dorsally and laterally, the ossifications do not always meet in the mid-like posteroventrally (see *Moythomasia*, Figs 8, 9, 10). A posterior notch in the floor of the foramen magnum in *Pteronisculus* (Nielsen 1942: 32) and *Kansasiella* (Poplin 1974: fig. 14) represents this unossified area in the Gogo palaeoniscids.

The upper margin of the occipital arch is occasionally produced anteriorly, partly closing the fontanelle, and this may represent a median supraoccipital. The extent of the supraoccipital is very uncertain in most specimens of *Mimia*, but can be more clearly discerned in *Moythomasia* (see Fig. 10). While there is no evidence of a supraoccipital in *Pteronisculus* (Nielsen 1942: fig. 7), *Kentuckia* (Rayner 1951: fig. 6) and *Australosomus* (Nielsen 1949: fig. 3), a median protuberance in *Kansasiella* (Poplin 1974: fig. 12; av.) and the closure of the posterior dorsal fontanelle in *Boreosomus* (Nielsen 1942: 286) support the idea that such a bone existed in these last-named forms at least. Elsewhere in primitive actinopterygians a supraoccipital is possibly present in *Perleidus* (Patterson 1975: 456), where its presence is inferred from the mode of closure of the uppermost part of the occipital fissure (posterior dorsal fontanelle).

The occipital region occupies less than 15% of the total neurocranial length measured through the vagus foramen and in this respect *Mimia* is similar to *Pteronisculus* (Nielsen 1942: fig. 4) and *Kansasiella* (Poplin 1974: fig. 13). The occipital region is much shorter in the pholidopleurid *Australosomus* (Nielsen 1949: fig. 2) and in the primitive teleost *Pholidophorus* (Patterson 1975: fig. 56). The occipital region is not as deep as the rest of the neurocranium, the greatest depth being attained immediately in front of the ventral otic fissure, much as in *Boreosomus* (Nielsen 1942: fig. 62).

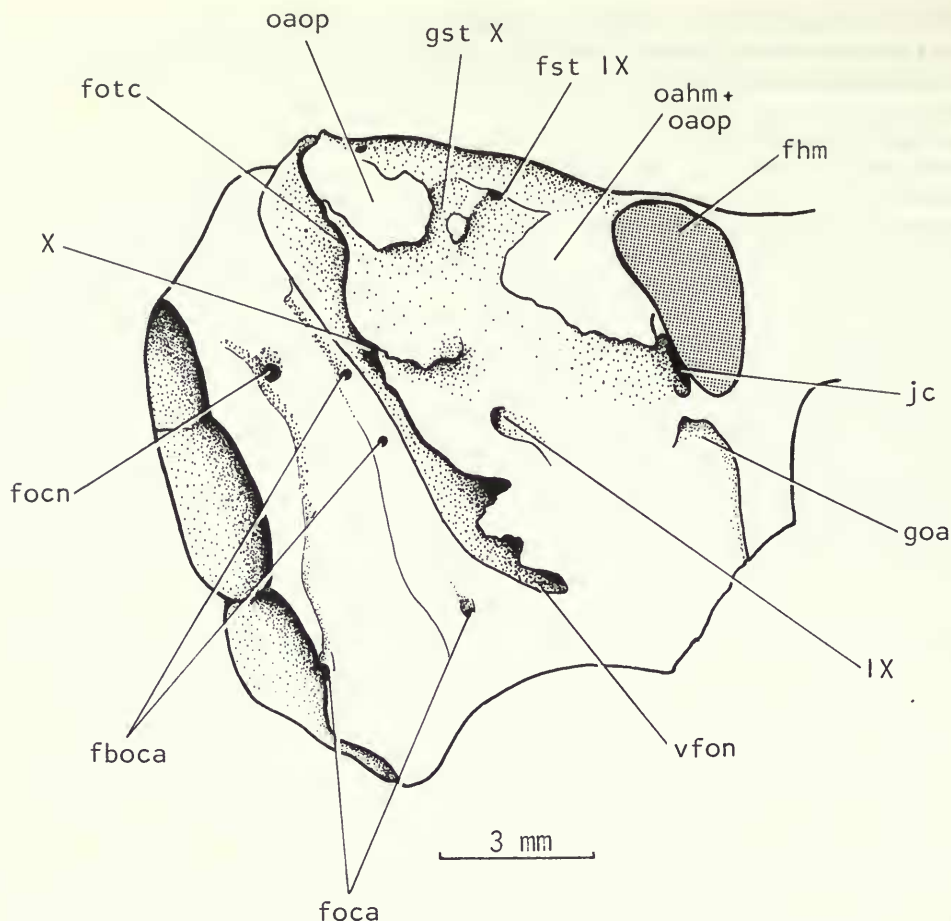


Fig. 5 *Mimia toombsi* Gardiner & Bartram. Otic and occipital regions in right lateral view, from BMNH P.53234.

The posterior face of the occiput (Figs 1, 2, 3) is broader above the foramen magnum than below, and the dorsal margin is gently rounded. The greatest width is at the level of the dorsal margin of the foramen magnum where the outline is more acutely rounded before the bone turns increasingly forwards and inwards to merge into the ventral surface. An acutely rounded dorsolateral prominence (Fig. 2) is assumed to be made up by the intercalar. This lies immediately posterodorsal to the vagus foramen and has been termed the cranio-spinal process by Nielsen (1942: 38). It is homologous with the cranio-spinal process in other palaeoniscids and chondrosteans such as *Saurichthys*, *Acipenser* and *Polydon*. Patterson (1975: 315) has shown that the intercalar in *Pholidophorus* is the homologue of the cranio-spinal process of chondrosteans but here, as in halecostomes, it received the ligament from the ventral limb of the post-temporal. No such ventral limb existed in palaeoniscids and there is no evidence of a ligament; there is likewise no such limb in chondrosteans though an extension from the post-temporal in *Acipenser* reaches the occipital process posterior to the vagal foramen (Jollie 1980: 240). (A limb does exist in *Polypterus* but this is inferred to have arisen independently of that in neopterygians). The cranio-spinal process is also found in acanthodians (Miles 1973a: 86) and placoderms (Stensiö 1969; Young 1980: fig. 8, infravagal process) and may be a primitive gnathostome attribute. Miles (1977: 55) has suggested that either the transverse process in dipnoans may be homologous with the cranio-spinal process, or it may be serially homologous

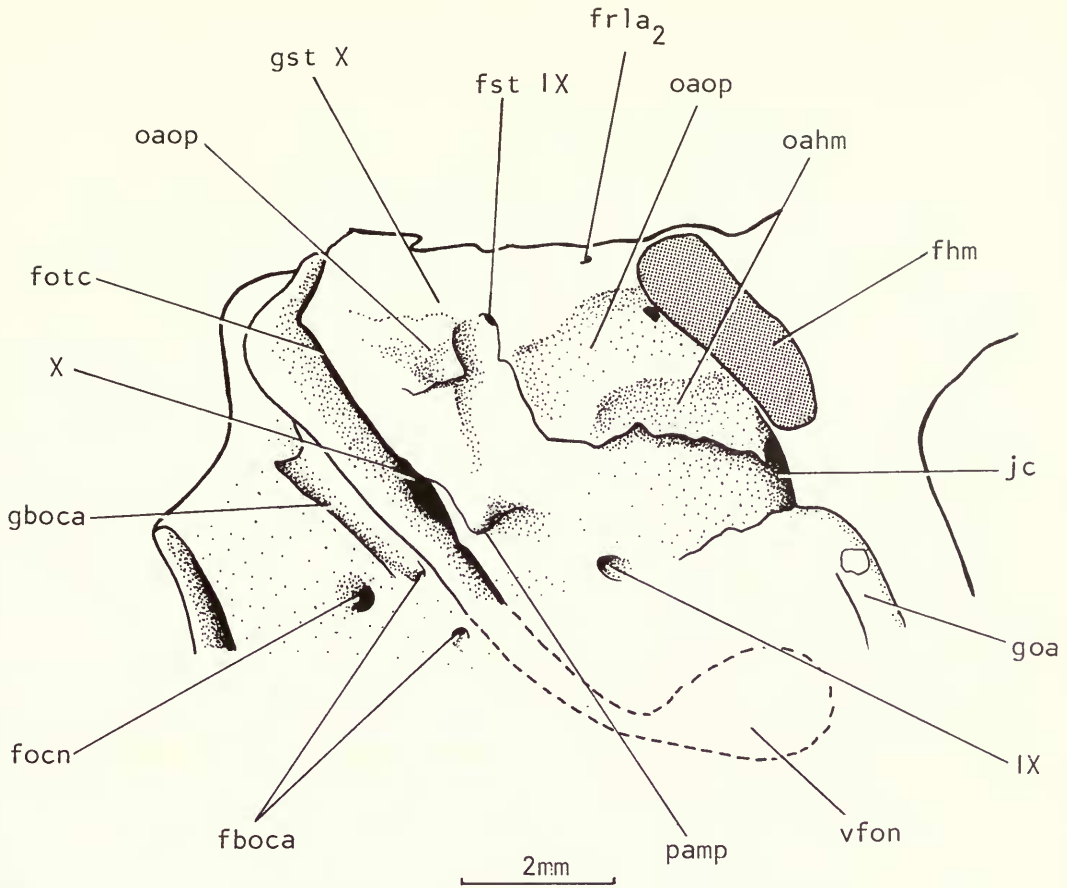


Fig. 6 *Mimia toombsi* Gardiner & Bartram. Dorsal portion of the otic and occipital regions in right lateral view, from BMNH P.56496.

with it if the cranio-spinal process represents an epineural. The first suggestion is unlikely since the intercalar lies in front of the first intermuscular septum in *Mimia* and forms part of the posterior margin of the occipital fissure as well as the hind margin of the foramen for the vagus nerve, whereas in fossil dipnoans the transverse process lies behind the third occipital nerve and so is quite distant from the vagus foramen and the occipital fissure. Separate epineurals are synapomorphous for teleosts. However, epineural processes are present on the anterior vertebrae of *Griphognathus* where they appear to ossify independently (Rosen *et al.* 1981: fig. 54A). Furthermore in *Neoceratodus* the cartilaginous transverse process serves as a boss for the articulation of a cranial rib. Thus the dipnoan transverse process seems more likely to be homologous with an epineural process than with the actinopterygian cranio-spinal process.

The foramen magnum is somewhat higher than it is broad (fm, Figs 1, 2, 3) and much smaller than the entrance to the notochordal canal. The notochordal canal (not, Figs 1, 2, 26) is ovoid in section, a little broader than high and with its long axis extending through the whole of the otic region and terminating in the top of the ventral otic fissure (Figs 16, 20, 26). The width of the notochordal canal diminishes rapidly in an anterior direction (Fig. 26) but then remains the same width up to the fissure. There is no real occipital condyle and the notochordal canal is not lined with a cone of perichordal tissue as in pholidophorids, leptolepids and Recent teleosts (Patterson 1975: 318).

Beneath the notochordal canal lies the aortic canal (cao, Figs 1, 2, 14, 15, 16, 25, 26, 50) which

is almost circular in section. The aortic canal leads forwards and downwards to open on the ventral surface on a level with the vestibular fontanelles. The walls of the canal are smooth, perichondrally lined and formed by the basioccipital. The aortic canal narrows somewhat anteriorly, then finally widens into a half-funnel shaped opening with two well-marked grooves diverging from the lateral margins of its mouth. These grooves (gla, Fig. 14) mark the paths of the lateral aortae. Just anterior to the point of bifurcation of the aorta (in BMNH P.53259) there is a small longitudinal crest which marks the point of attachment of the aortic ligament (alig, Figs 14, 50). In other specimens of *Mimia* and in *Moythomasia* this crest is replaced by a small protuberance (Gardiner 1973: fig. 2; sup) in the same position or occasionally placed more anteriorly, that is more distant from the point of bifurcation. The dorsal aorta bifurcated level with the anterior end of the vestibular fontanelle.

In one specimen of *Mimia* (BMNH P.53259, Fig. 15) the aortic canal itself bifurcates anteriorly, as in *Polypterus*, and here the aortic ligament must have originated on the pillar which divides the canal. In this specimen the point of bifurcation lies behind the level of the vestibular fontanelle. In *Kansasiella* (Poplin 1974: fig. 14) the aortic canal is much longer than in *Mimia*; it bifurcates anteriorly (as in P.53259), but additionally has a paired opening in the floor of the canal for the exit of the second efferent arteries. The aortic canal is also very long in *Boreosomus* (Nielsen 1942: fig. 63) but here both the anterior opening and the opening in the floor of the canal (for the second efferents) are unpaired. In *Pteronisculus* (Nielsen 1942: fig. 6) and *Kentuckia* (Rayner 1951: fig. 4) the canal is long, the anterior opening bifurcated, but the opening in the floor single. *Cosmoptychius* (Schaeffer 1971: fig. 8) has a long canal bifurcated anteriorly with no apparent ventral opening.

In pholidopleurids such as *Australosomus* the aortic canal is much shorter, but there is still a well-marked median peg-like process for the attachment of the aortic ligament (Nielsen 1949: figs 5, 6). A similar process (alig, Fig. 7 and see p. 201) can be seen in *Moythomasia* although the aortic canal is much longer.

The wall of the aortic canal is perforated by a large dorsolaterally-directed canal which transmitted the occipital artery (foca, Figs 1, 2, 13, 14, 15). In most specimens there is a single foramen on either side, but in some (BMNH P.53250 for example) there is a single opening for the occipital artery on one side and a double opening on the other, while in other specimens the canal is double on both sides (foca, Figs 4, 5). Allis (1922: 207) described a blind canal in the basi-exoccipital of *Polypterus* in the position of the occipital artery in *Amia* and *Mimia*, but he also showed how the succeeding two intervertebral arteries in *Polypterus* arise as a single artery from the dorsal aorta, then branch into two, the anterior branch passing up (presumably) in relation to the intermuscular septum and the more posterior passing into the cranial cavity through the occipital nerve foramen.

Elsewhere within palaeoniscids and pholidopleurids there is always a dorsolaterally-directed canal for the occipital artery, single in *Pteronisculus* (Nielsen 1942: fig. 9), *Kansasiella* (Poplin 1974: fig. 20) and *Australosomus* (Nielsen 1949: fig. 4) but double in *Kentuckia* (Rayner 1951: figs 4, 7). Although there are two openings on either side for the occipital arteries in *Parasemionotus* (Lehman 1952: fig. 3), in the majority of more advanced actinopterygians the occipital artery, where it occurs, issues through a single opening on either side of the aortic canal or groove (*Lepidotes* Patterson 1975: fig. 109; *Dapedium* Patterson 1975: fig. 113; *Amia* Allis 1897: 706; *Pachycormus* Patterson 1975: fig. 106; pholidophorids Patterson 1975: 320).

At the anterior end of the basioccipital, a small paired perichondrally-lined canal passes anteroventrally down through the bone from a point in the floor of the neurocranium (VI₂, Fig. 25) at the level of the anterior end of the zygial plate (see below, p. 194) to open ventrally in the floor of the orbit dorsolateral to the ventral otic fissure (Figs 16, 20). As it passes into the floor of the orbit this canal enters the ventral edge of the prootic (this can be inferred from BMNH P.53245 in which the perichondral margin of the prootic just encloses the anterior limit of the canal). This canal must have transmitted the abducens nerve (VI, Fig. 29). In one specimen (BMNH P.53234, Fig. 25) the canal is forked dorsally within the basioccipital and each branch is continuous with a short canal in the zygial plate. The cranial entrance to these canals is a pair of oval foramina on the medial surface of each zygial (a similar pair of foramina is also present in

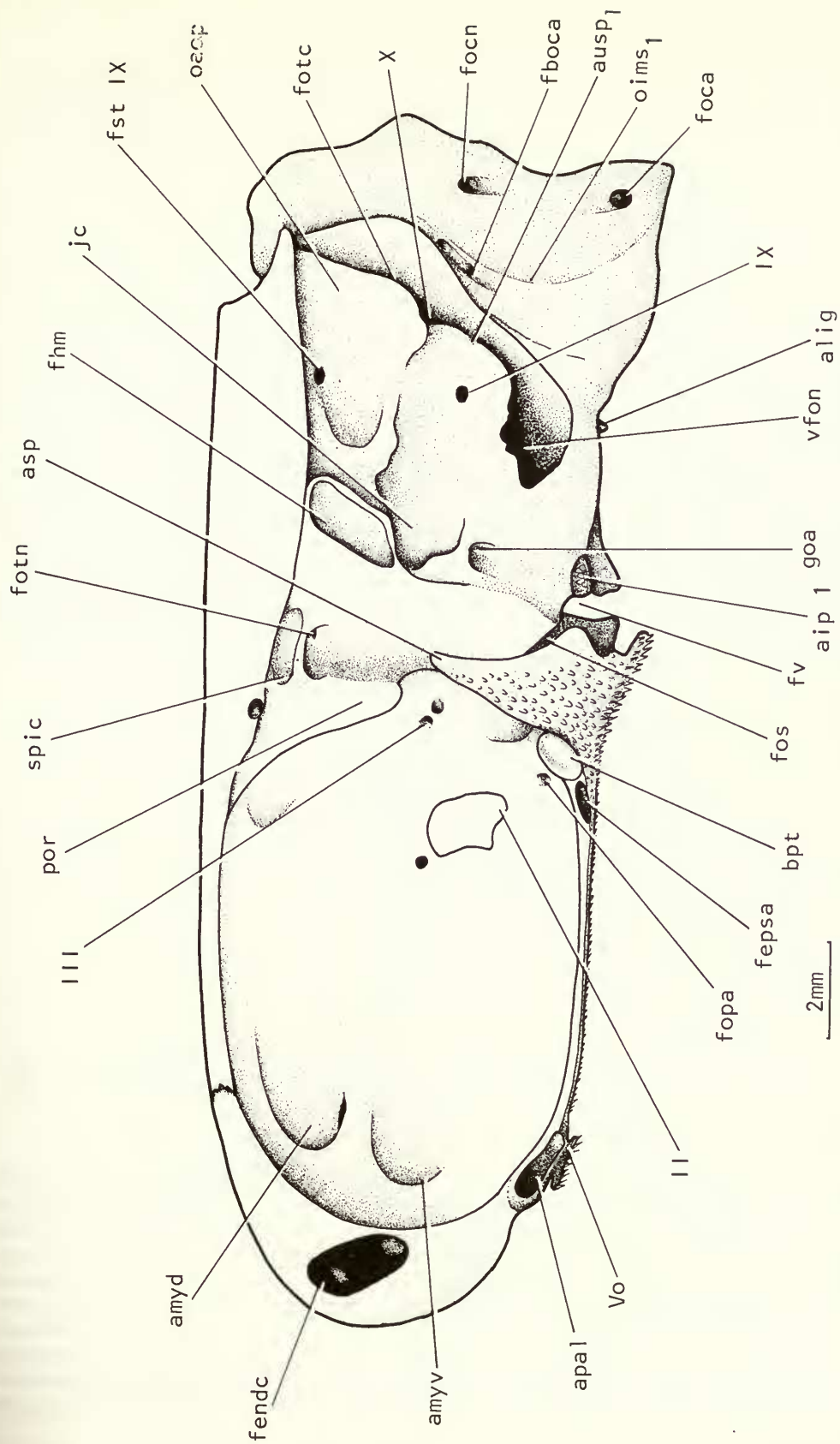


Fig. 7 *Moythomasia durgaringa* Gardiner & Bartram. Neurocranium in left lateral view. Composite, based on several specimens.

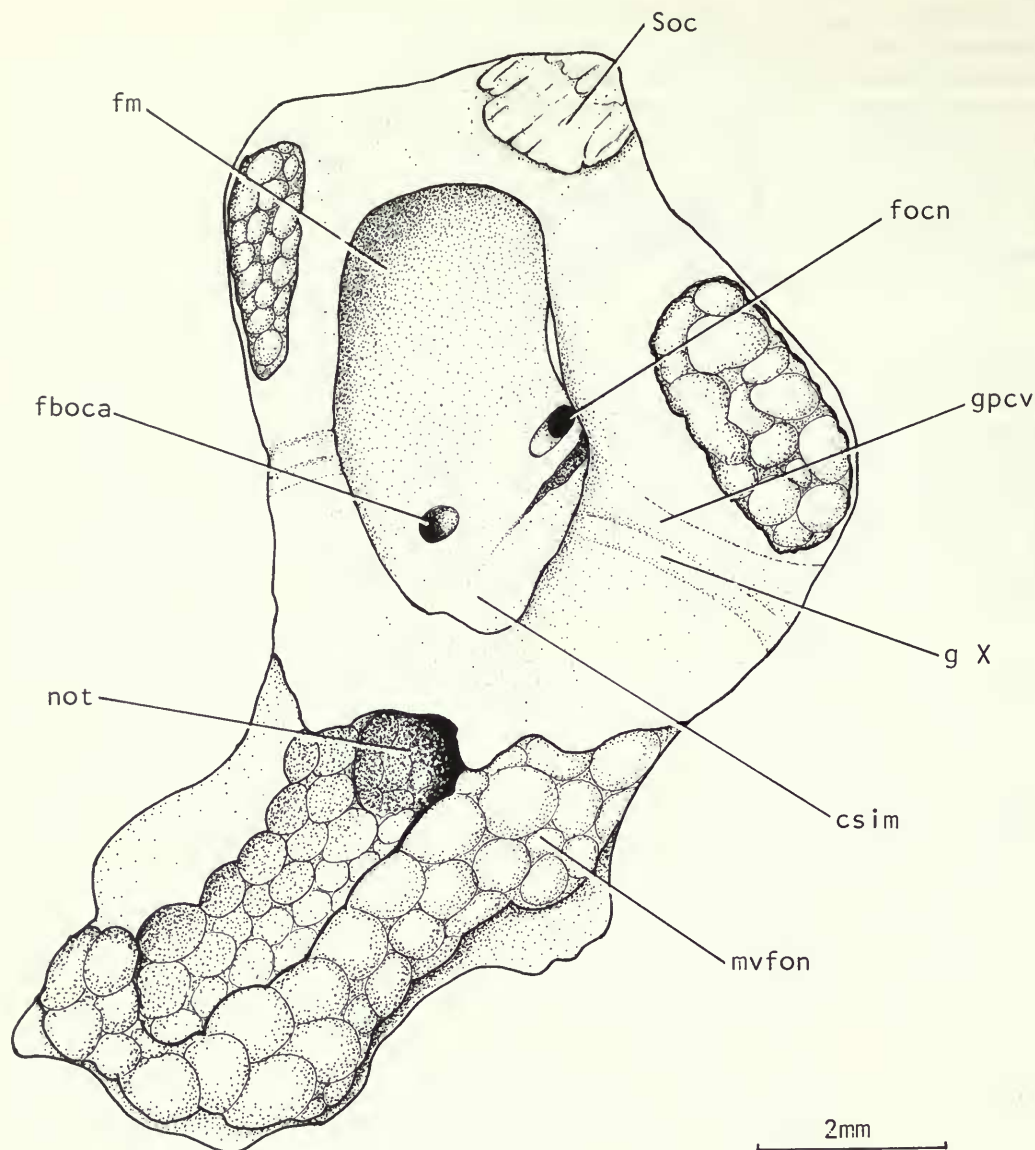


Fig. 8 *Moythomasia durgaringa* Gardiner & Bartram. Occipital region in anterodorsal view, looking into the rear of the vestibular fontanelle from the left side, from BMNH P.53221.

BMNH P.53249). In all living actinopterygians the root of the abducens nerve is double, but in this particular specimen (BMNH P.53234) of *Mimia* the two roots remained separate until they entered the basioccipital. In all other specimens examined the canal for the abducens nerve opens below the zygial plate. However, when there is a single short canal in the posterior region of the zygial, it is always in direct line with the internal opening of the abducens canal. Rayner (1951: fig. 10) suggested that a similar foramen in the zygial plate of Watson's palaeoniscid *A* served to transmit the abducens nerve. In *Polypterus* (Allis 1922: 228) the canal for the abducens opens in the floor of the cranial cavity immediately posterior to the base of the cartilaginous prootic bridge and runs anteriorly in the cartilage between the basi-exoccipital and basisphenoid, to open by a notch in the edge of the basisphenoid immediately below the

trigeminal foramen. Thus the relationship of the abducens is similar in *Mimia* and *Polypterus* except that in the latter the prootic ossification is absent. In other palaeoniscids and pholidopleurids the abducens nerve never passes through the basioccipital. Instead it always leaves the cranial cavity in front of the ventral otic fissure, usually through the prootic bridge (*Pteronisculus* Nielsen 1942: figs 9, 10; *Kentuckia* Rayner 1951: fig. 8, *Kansasiella* Poplin 1974: fig. 23; *Australosomus* Nielsen 1949: fig. 7). In halecostomes such as *Amia*, pholidophorids and most Recent teleosts the abducens nerve passes through the prootic bridge (formed by the prootics into the roof of the myodome. Primitively in actinopterygians the abducens nerve is deduced to have passed through the basioccipital for part of its course, but with rearward migration of the ventral otic fissure this relationship was lost.

The zygial plates arise from the anterior ends of the walls of the notochordal canal and are more or less contiguous with the underlying basioccipital. They rise upwards and outwards at an angle of perhaps 70° and are occasionally joined in the mid-line ventrally by a thin strut of endochondral bone (in the roof of the notochordal canal). In BMNH P.53249, in which much of the internal, perichondral margin of the prootic has not yet fused with adjacent bones (Pro, Fig. 25), the separate nature of the paired zygals can be recognized. They are delicate ossifications completely covered in perichondral bone except along their ventral margins where they are partially fused to be basioccipital. Sometimes there is a small posterior foramen in each zygial, occasionally two foramina, one anterior and one posterior (VI₁, VI₂, Fig. 25; see also Fig. 26). These foramina transmitted the abducens nerve from the floor of the brain into the adjacent canal in the basioccipital. Dorsally each zygial has a distinct notch in its margin; this presumably served for the passage of the auditory nerve from the brain to the otic capsule. That these plates really are separate ossifications can be inferred from the limits of their perichondral covering and from the nature of their endochondral core, which is made up of very small units quite

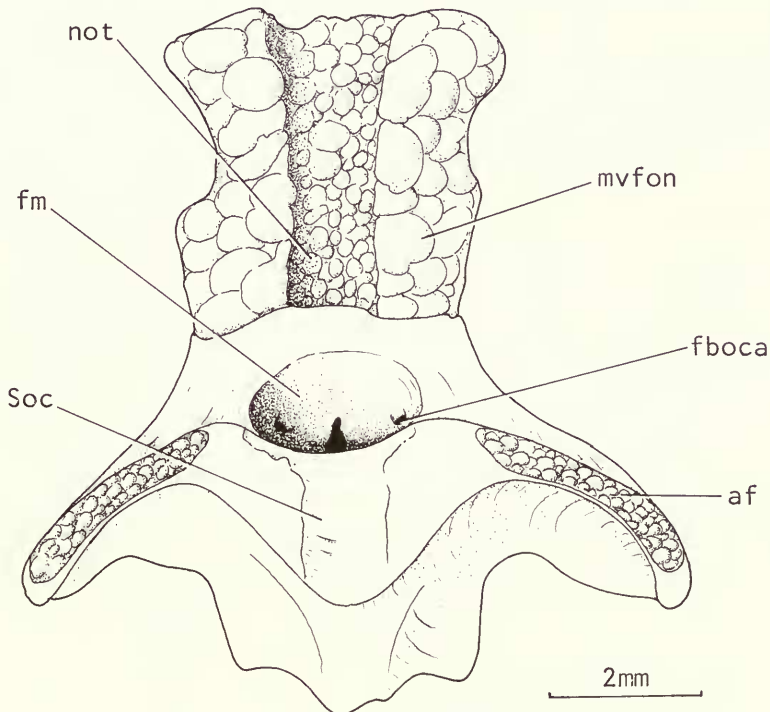


Fig. 9 *Moythomasia durgaringa* Gardiner & Bartram. Occipital region in antero-dorsolateral view, looking into the floor and rear of the vestibular fontanelle from BMNH P.53227.

dissimilar from the large 'bubbles' of bone making up the underlying basioccipital. These plates form the inner wall of the pocket that housed the sacculus, separating it from the floor of the brain. In *Polypterus* a cartilage in a similar position performs the same function. The relationships of these plates to the sacculus can best be seen in a reconstruction of an endocranial cast of *Kansasiella* (Poplin 1974: fig. 23). Zygals plates have previously been recorded in only one other actinopterygian, *Pteronisculus* (Nielsen 1942: fig. 9, om; Bjerring 1971: fig. 6), but they are also recognizable in *Kentuckia* (Rayner 1951: 70 – median projection) and *Kansasiella* (Poplin 1974: fig. 20, t).

In *Pteronisculus* (Nielsen 1942: 53) the displaced zygals plate is obviously a separate ossification since it has no connection with any other bone. Presumably it formed above the notochord and occupied a similar position in life to that in *Mimia*. It is a small, horizontal, bilaterally symmetrical plate, devoid of perichondral lining ventrally. In both *Kentuckia* and *Kansasiella* the zygals plate is shown as a median ossification in the roof of the notochordal canal and is inseparable from the underlying basioccipital, but produced dorsolaterally into perichondrally-lined wings, very similar to the paired zygals plates in *Mimia*. From these four examples it is not possible to decide whether paired or unpaired zygals represent the more primitive condition, but certainly the presence of zygals is primitive (see p. 207) both for actinopterygians and osteichthyans.

Externally the surface of the occipital region around the notochordal canal and foramen magnum is marked by two distinct parallel ridges which run vertically up the lateral walls of the neurocranium. The more posterior ridge starts on the aortic canal just behind the foramen for the occipital artery and runs in a more or less uninterrupted line to fade out dorsally on a level with the middle of the foramen magnum, posterodorsal to the foramen for the occipital nerve. This ridge marks the origin of the second intermuscular septum (oims₂, Figs 1, 2, 3, 4). The more anterior of the two ridges also commences on the aortic canal. It is considerably more elevated than the posterior ridge and continues further dorsally and finally peters out well above the foramen magnum. The first intermuscular septum presumably originated (oims₁, Figs 1, 2, 3, 4) on this ridge.

In those specimens with only one opening for the occipital artery (BMNH P.53243, Fig. 2) a groove leads anterodorsally from that foramen towards the foramen for the occipital nerve. A little below the occipital nerve foramen the groove bifurcates and the anterior branch proceeds almost horizontally through a gap in the ridge for the first intermuscular septum to pass

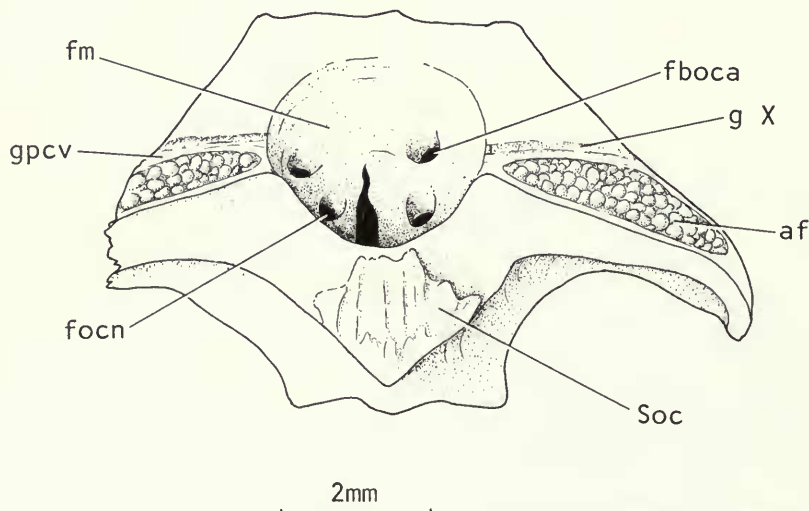


Fig. 10 *Moythomasia durgaringa* Gardiner & Bartram. Dorsal part of the occipital ossification in anterodorsal view, from BMNH P.53221.

immediately into the mouth of a small foramen (fboca, Fig. 2) which gives direct access to the floor of the cranial cavity, anterior to the occipital nerve (see *Moythomasia*, fboca, Figs 8, 9, 10). This short canal runs longitudinally through the bone, and clearly transmitted a blood vessel rather than a nerve. From the disposition of the groove leading to it, the canal must have carried a branch of the occipital artery into the rear of the cranial cavity. The other branch of the groove passes up and turns anterodorsally just below the occipital nerve foramen, passes through a more dorsal notch in the ridge for the first intermuscular septum (gboca, Figs 2, 3), and continues as a groove onto the dorsal surface of the occiput. In one specimen (BMNH P.56496), and on one side only, this dorsal branch passes through a distinct foramen in the ridge (fboca, Fig. 3) for the first intermuscular septum. This dorsal branch must have supplied blood from the occipital artery to the first trunk muscle.

Where there is a double opening for the occipital artery the more anterior opening always lies in front of the ridge for the first intermuscular septum (BMNH P.56501 and P.53234, Figs 4, 5). In these specimens a gutter runs directly from this anterior opening to the entrance of the canal which passes into the cranial cavity (fboca, Figs 4, 5). There can be no doubt here that the canal which opens into the cranial cavity transmitted a branch of the occipital artery. Moreover in these specimens, as the canal for the branch of the occipital artery passes horizontally through the wall of the neurocranium, it gives off another branch dorsally. This branch emerges on the lateral wall on a level with the foramen for the occipital nerve and from its mouth an even more distinct gutter (gboca, Figs 4, 6) runs up onto the dorsal occipital surface. This foramen and gutter carried a branch of the occipital artery to the first trunk muscle, and presumably is equivalent to the dorsal branch of the occipital artery in those forms where the occipital artery is single.

In the inner wall of the foramen magnum there are two foramina, the more anterior of which transmitted the branch of the occipital artery. The more posterior foramen is the larger and the canal from it runs posterolaterally to open just in front of the ridge for the second intermuscular septum. This canal transmitted an occipital nerve (focn, Figs 1, 2, 3, 4, 5, 6, 13). In the floor of the foramen magnum, level with the foramen for the branch of the occipital artery, is a shallow paired depression (see *Moythomasia*, csim, Fig. 8) but whether or not this can be regarded as an incipient cavum sinus imparis depends on interpretation. A more obvious median depression is seen in the palaeoniscid *Pteronisculus* (Nielsen 1942: fig. 5), but the true extent of the cavum sinus imparis is perhaps only seen in teleosts (Patterson 1975: 316). If, however, a vascular plexus did exist primitively in the floor of the foramen magnum then a direct arterial supply would have been an advantage.

Remnants of this rather elaborate occipital arterial blood supply can be recognized in several later forms. Patterson (1975: 292) has described in *Pholidophorus* a dorsolaterally-directed canal which originates in the cranial cavity immediately in front of the occipital nerve and opens on the dorsolateral surface of the exoccipital. This canal anastomoses (within the bone) with an anteriorly-directed canal which opens in the upper part of the vagus canal. Patterson (*ibid.*) suggested that the anterior branches carried a tributary of the posterior cerebral vein while the dorsolaterally-directed canal carried both a vein and a branch of the occipital nerve. There seems little doubt that the dorsolaterally-directed canal is homologous with a similar canal in *Mimia* which, as shown above, served for a branch of the occipital artery. On the other hand in *Pteronisculus* (Nielsen 1942: 38, fig. 5) there is a canal running from the foramen magnum to the hind wall of the vagus canal. This appears to be homologous with the anteriorly-directed canal in *Pholidophorus*. Further, Nielsen (1942: 35) described a possible connection between this canal and a more ventral canal which opens on the occipital surface near the occipital artery (Nielsen 1942: fig. 4, k). In one specimen of *Mimia* (BMNH P.53245) there is, on one side only, a similar connection within the bone between an anteriorly-directed canal which opens in the upper part of the vagus canal and the canal carrying a branch of the occipital artery into the cranial cavity. Thus it is likely that the anteriorly-directed canal in *Pteronisculus* and *Pholidophorus* transmitted yet another branch of the occipital artery. Bjerring's (1971: fig. 6) suggestion that this canal in *Pteronisculus* transmitted a hypothetical branch of the abducens nerve which innervated the subcranial muscle is without foundation (see also Patterson 1975: 294).

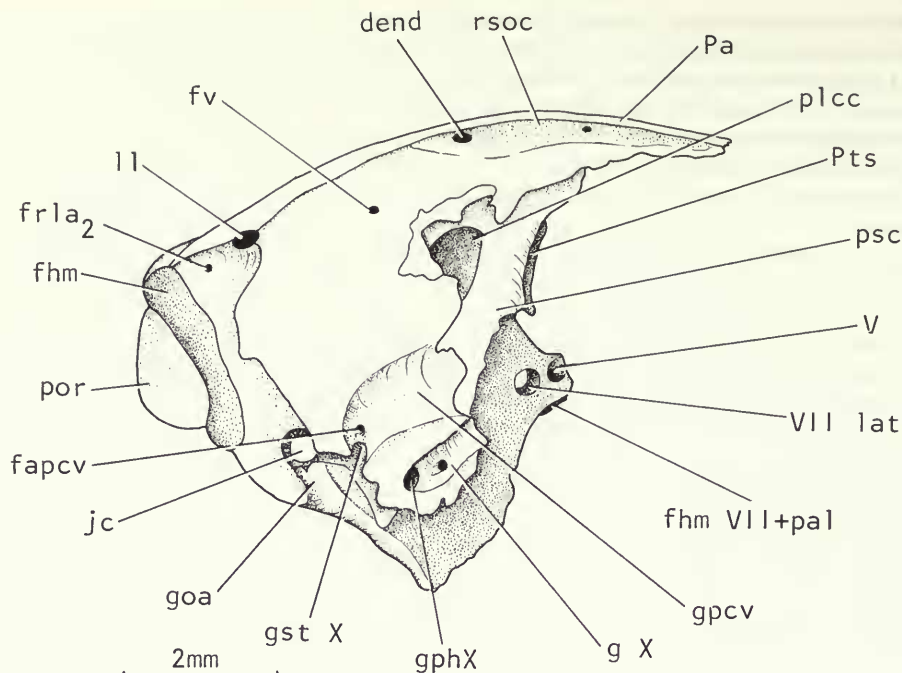


Fig. 11 *Mimia toombsi* Gardiner & Bartram. Left half of otic region of the neurocranium and attached dermal bones in posterior view, from BMNH P.53245.

A dorsolaterally-directed canal originating in the floor of the foramen magnum and opening on the occipital roof is also present in parasemionotids (Patterson 1975: fig. 97), *Caturus* (Patterson 1975: 319), '*Aspidorhynchus*' (Patterson 1975: fig. 100) and *Heterolepidotus* (Patterson 1975: fig. 104). Presumably in all these cases it carried a branch of the occipital artery.

Apart from *Mimia* (and perhaps *Pteronisculus*) the only other palaeoniscid in which a branch of the occipital artery passes directly into the cranial cavity is *Kansasiella* (Poplin 1974: fig. 19, spi).

A single occipital nerve canal as seen in *Mimia* is characteristic of most palaeoniscids (*Pteronisculus*, *Boreosomus*, *Kentuckia*, *Kansasiella*), *Australosomus*, parasemionotids, pholidophorids and leptolepids (Patterson 1975: 319) and is considered to be the primitive condition for actinopterygians. Although this single occipital nerve corresponds to the first occipital nerve of *Polypterus*, *Acipenser*, *Polyodon*, *Lepisosteus* and *Amia*, all these forms have incorporated one or more neural arches and corresponding spino-occipital nerves into the braincase. Similar incorporations are deduced to have occurred in *Birgeria*, *Saurichthys*, *Lepidotes* and *Dapedium* (Patterson 1975: 319).

No real evidence for the position of intermuscular septa has previously been produced in palaeoniscids. In fact the only previous record of septal position in fossil actinopterygians is from pholidophorids. On the epioccipital of *Pholidophorus germanicus* (Patterson 1975: 297) a posteriorly-projecting shelf of membrane bone marks the point of origin of the first intermuscular septum, while just behind the external opening of the occipital nerve canal a large trifid projection marks the origin of the second intermuscular septum, much as in *Amia* (Allis 1897) and *Scomber* (Allis 1903). These projections in *Pholidophorus*, *Amia* and *Scomber* are homologous with the more complete ridges in *Mimia*.

The dorsal face of the occiput above the foramen magnum slopes gently upwards in the mid-line, then at the level of the external opening of the occipital nerve canal it rises steeply to a short median crest. The ridge so formed is not as pronounced as the so-called crista occipitalis of

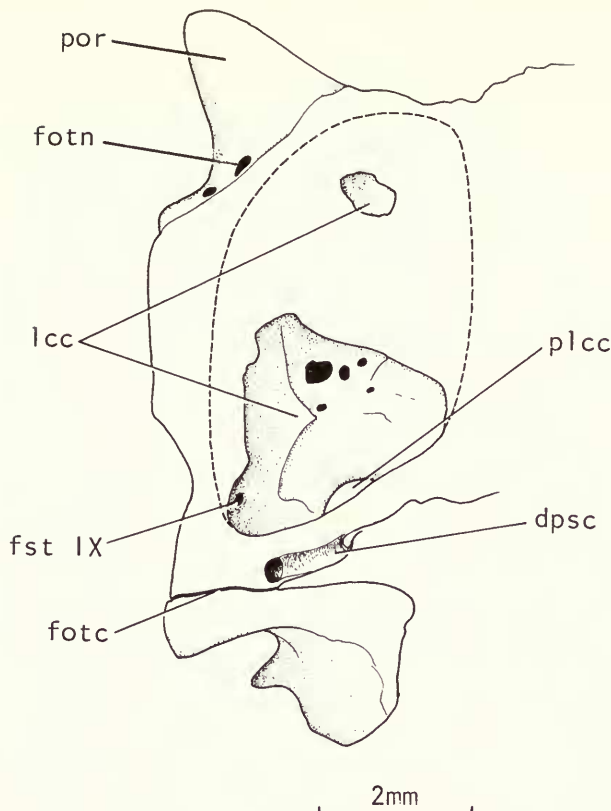


Fig. 12 *Mimia toombsi* Gardiner & Bartram. Left otic and occipital regions of the neurocranium in dorsal view, from BMNH P.53234. The broken line marks the limits of the lateral cranial canal.

Pteronisculus (Nielsen 1942: fig. 3) or *Kansasiella* (Poplin 1974: fig. 13). Dorsally, just below the supraoccipital, the crest gives way to a triangular prominence which presumably served for the insertion of the longitudinal intervertebral ligament (ivl, Figs 1, 2, 3). In one specimen (BMNH P.53245) the triangular prominence is missing and instead there is a prominent median ridge. Elsewhere in fossil actinopterygians, a distinct cartilage-lined pit in the exoccipital region above the foramen magnum is seen in parasemionotids (Patterson 1975: fig. 98) and in *Dapedium* (Patterson 1975: fig. 113); this marks the insertion of the longitudinal ligament in those fishes. On either side of the median crest in *Mimia* two distinct depressions mark areas of origin of the anterior trunk muscle (oatm, Figs 1, 2, 3).

The canal for the vagus and the nervus lineae lateralis is represented by an inflated part of the occipital fissure. The internal opening of the canal lies some distance above the floor of the foramen magnum from whence it passes posterolaterally to exit immediately posteriorly to the parampullary process. The posterior wall of the vagus canal is divided by a narrow ridge into two roughly equal divisions. The upper division contained the posterior cerebral vein (gpcv, Fig. 11) and the lower the vagus nerve (g.X, Fig. 11), as in *Saurichthys* (Stensiö 1925: fig. 4), *Pteronisculus* (Nielsen 1942: 39) and *Pholidophorus* (Patterson 1975: 293).

Moythomasia durgaringa

The occipital region in this species is very similar to that of *Mimia* and only the salient differences will be noted.

The posterior dorsal fontanelle is perichondrally lined and larger than in *Mimia* (Gardiner 1973: fig. 7). The occipital fissure is more steeply inclined and the vestibular fontanelle much

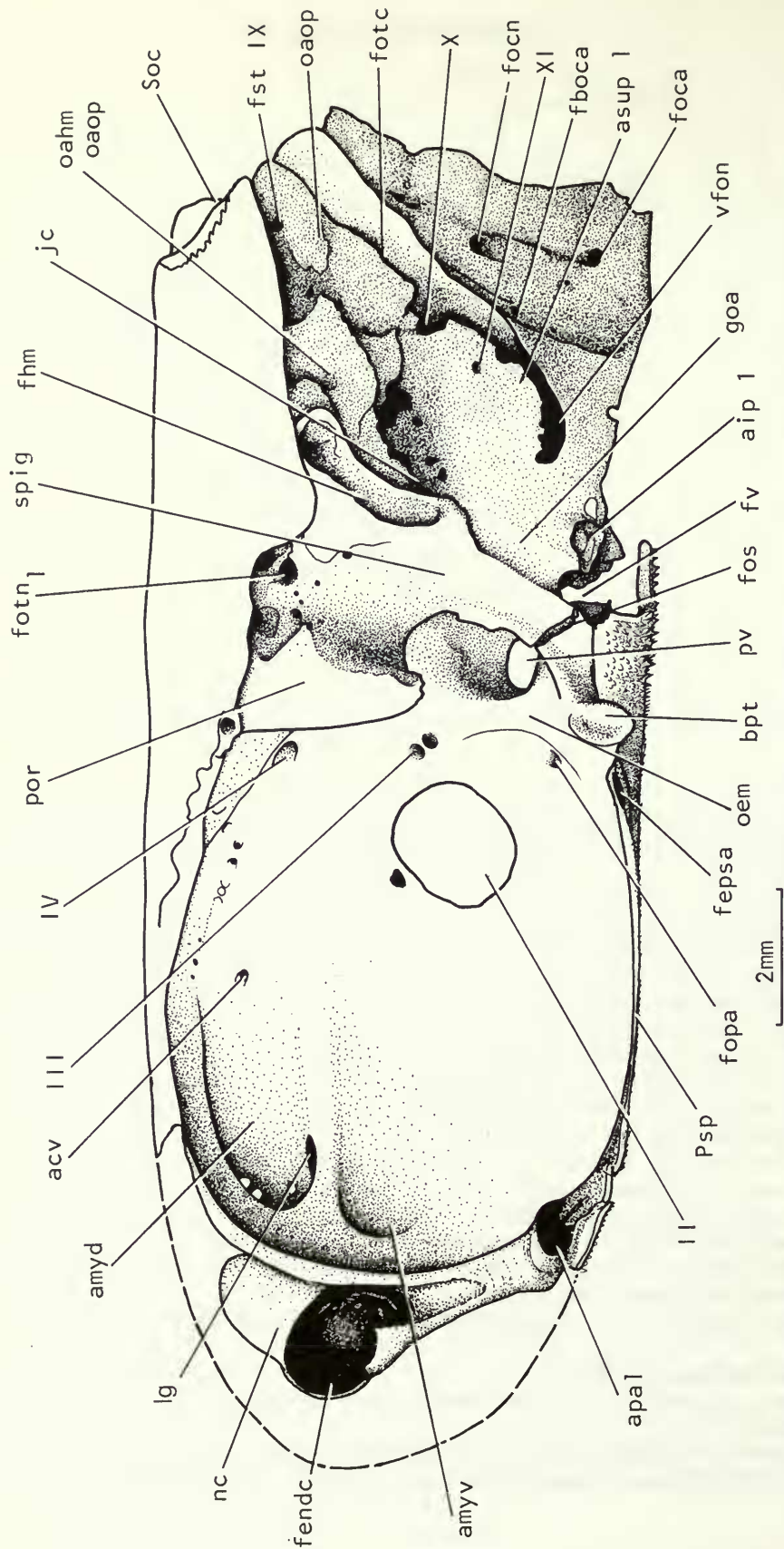


Fig. 13 *Mimia toombsi* Gardiner & Bartram. Neurocranium in lateral view, from BMNH P.56498 (partly after Gardiner & Bartram 1977).

larger than in *Mimia*, nearer in size to that of *Pteronisculus*. The occipital fissure is perichondrally lined except for a large oval area between the vagus canal and supraoccipital (Figs 8, 9, 10).

The ventral otic fissure occupies a similar position to that in *Mimia* although it is not quite as extensive dorsomedially (fv, Fig. 29). The occipital region occupies less than 17% of the total neurocranial length (measured through the vagus foramen) and, unlike *Mimia*, is higher than any other portion. A more clearly definable centre of ossification, presumably representing the supraoccipital, can be recognized in some specimens (BMNH P.53221) but the cranio-spinal process is a little more ventral than in *Mimia*, level with the bottom of the foramen magnum. The foramen magnum is marginally wider than high while notches in the hind ventral wall of the notochordal canal similar to those in *Mimia* show ossification to be incomplete in these areas. The aortic canal is similar in shape and size to that of *Mimia* but the peg-like process for the attachment of the aortic ligament (alig, Fig. 7) is much more prominent and more posterior in position, lying immediately in front of the anterior opening of the aortic canal. The wall of the aortic canal is perforated by a single, dorsolaterally-directed canal for the occipital artery, but even though the ridge for the insertion of the second intermuscular septum is not as distinct as in *Mimia*, the course of the occipital artery is clear. A groove leads up from the foramen for the occipital artery (BMNH P.53221) towards the foramen for the occipital nerve, and just below this latter foramen the groove branches. One branch passes anteriorly, leads through a gap in the ridge for the first intermuscular septum, and immediately enters a small foramen from which a canal runs horizontally inwards to open in the anterior floor of the foramen magnum (fboca, Figs 8, 9, 10). As in *Mimia*, this canal must have transmitted a branch of the occipital artery into the floor of the cranial cavity. The other branch of the groove passes anterodorsally through a more dorsal gap in the ridge for the first intermuscular septum, then up towards the top of the occiput. Each of these paired grooves terminates in a foramen on either side of the mid-line, below the insertion of the intervertebral ligament. Each foramen connects, by means of a short anteroventrally-directed canal, with the cranial cavity above the foramen magnum. In one specimen (BMNH P.51380, Gardiner 1973: fig. 7) the two grooves terminate in a single foramen, set just off centre, below the insertion of the intervertebral ligament. These dorsal grooves and foramina transmitted a second branch of the occipital artery into the dorsal half of the cranial cavity. The only other osteichthyans in which similar dorsal openings have been described are the Devonian dipnoans *Griphognathus* and *Chirodipterus* (Miles 1977: figs 12, 16, nut) but in these forms the canals end blindly in the cranial bone.

In the floor of the foramen magnum, anterior to the opening for the branch of the occipital artery, there is a shallow paired depression which possibly housed the cavum sinus imparis. Normally, the floor of the foramen magnum posterior to this depression is unossified in the mid-line (Fig. 8) but in one specimen (BMNH P.56502) the floor is complete and raised in a distinct median ridge which runs from the depression to the hind margin of the foramen magnum. In some specimens a small foramen in the groove for the posterior cerebral vein (BMNH P.56502) could have transmitted another branch of the occipital artery. Dorsally, below the supraoccipital, a well-marked triangular area with several small protuberances must have served for the insertion of the intervertebral ligament.

Occipital region: discussion

1. *Posterior dorsal fontanelle*. A distinct posterior dorsal fontanelle seems to be confined within actinopterygians to the palaeoniscids and chondrosteans such as *Acipenser* (Bridge 1878), although Patterson (1975: 307) has suggested that an imperfectly ossified area in front of the supraoccipital in *Pholidophorus bechei* represents the remains of a small, paired posterior dorsal fontanelle. Elsewhere a distinct posterior dorsal fontanelle is seen in the rhipidistian *Eusthenopteron* (Jarvik 1954: figs 21B, C), where it appears as a crescent-shaped opening in the roof of the supraotic cavity, and in *Acanthodes* (Miles 1973a: fig. 3), where it is similar in shape and size to that in *Mimia*. Whether this is a true dorsal fontanelle in *Acanthodes* or merely a cartilaginous area devoid of perichondral ossification could not be determined. Miles (1977: 101) has convincingly homologized the posterior dorsal fontanelle of *Eusthenopteron* with openings

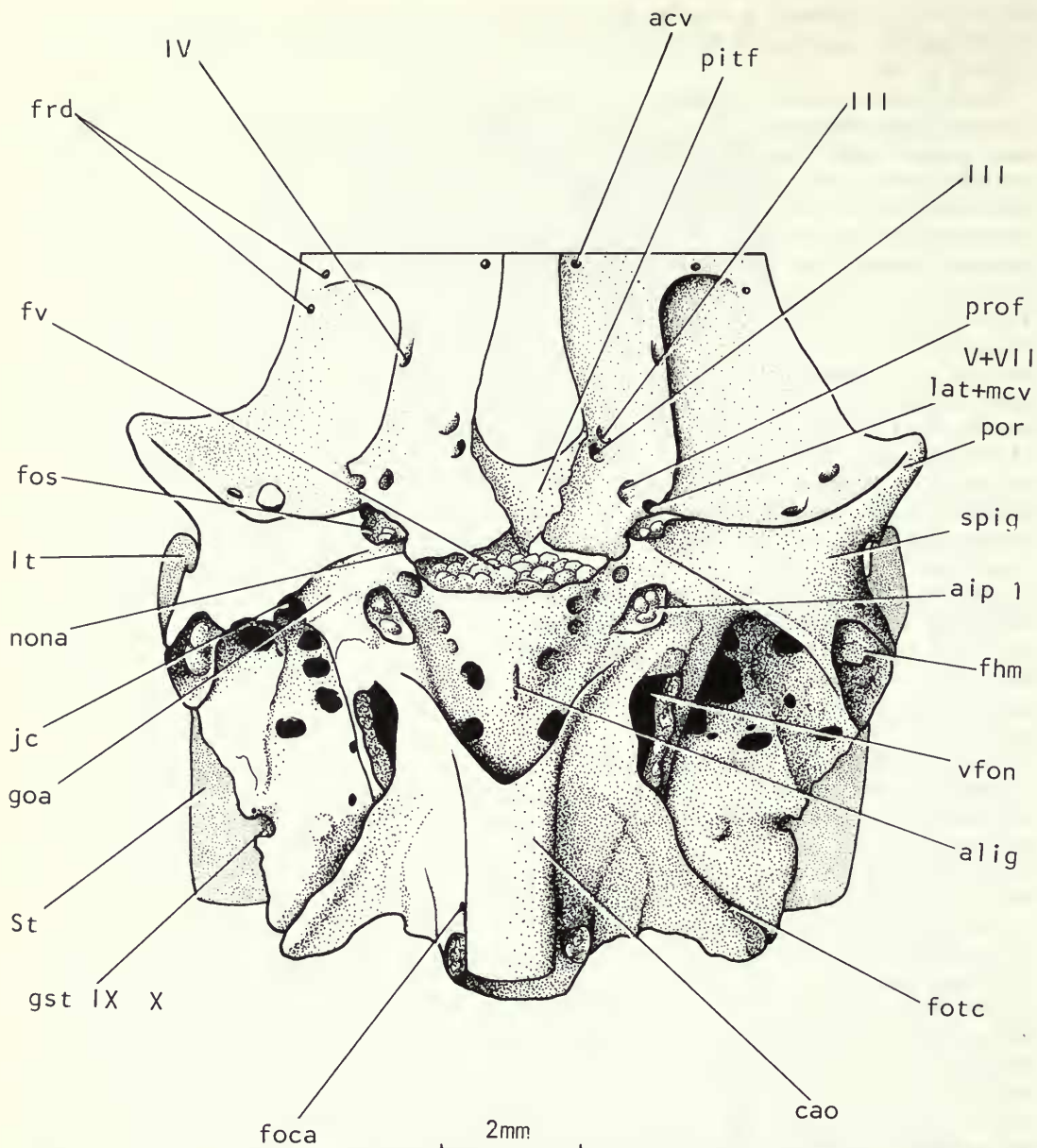


Fig. 14 *Mimia toombsi* Gardiner & Bartram. Occipital, otic and orbitotemporal regions of neurocranium and attached dermal bones in ventral view, from BMNH P.53259. Parasphenoid and basisphenoid missing.

of the paired endolymphatic ducts in the dipnoans *Griphognathus* and *Chirodipterus*, which differ from Recent dipnoans in having an external opening for the endolymphatic duct on the dermal skull roof. It is possible that in gnathostomes the posterior dorsal fontanelle primitively served for the exit of the endolymphatic ducts to the surface of the chondrocranium, since in xenacanth sharks (Schaeffer 1981: 22) the unpaired, slit-shaped endolymphatic fossa is confluent with the occipital fissure, and in *Moythomasia* the paired endolymphatic ducts open into the dorsal fontanelle.

2. *Occipital fissure*. Apart from palaeoniscids a completely uninterrupted, perichondrally-lined occipital fissure is only known in the pholidopleurid *Australosomus* (Nielsen 1949, Beltan 1968) and in the teleost *Pholidophorus* (Patterson 1975: 417). However, in the latter there is no obvious posterior dorsal fontanelle and parts of the fissure may be covered superficially by membranous outgrowths from the intercalar and supraoccipital. In *Perleidus* cf. *stoschiensis* (Patterson 1975: 460) the fissure is still perichondrally lined from the vagus canal up to the medial margin of the epioccipital and pterotic.

Not surprisingly perhaps, remnants of this perichondrally-lined fissure can be seen in several other actinopterygian groups. Within the amioids and in some parasemionotids (Patterson 1975: 434) the perichondral lining persists from the vagus canal to just above the external semicircular canal, while in some pachycormids (Patterson 1975: 448) a small area opposite the medial part of the intercalar is perichondrally lined. In the earliest known leptolepid braincase, from the Sinemurian, the perichondrally-lined portion of the cranial fissure still extends from the vagus canal up to the lower margin of the epioccipital.

Patterson (1975: 418) has shown how the occipital fissure is closed in pholidophorids, leptolepids and several other groups of actinopterygians by three distinct processes: obliteration of parts of the fissure by cartilage (this requires simple ontogenetic fusion of the occipital arch with the otic capsule prior to ossification), obliteration by forward extension of the occipital bones into the otic region, or the development of membrane bone outgrowths to bridge the fissure. In living chondrosteans the occipital fissure is obliterated by cartilage in *Acipenser*, and in *Polypterus* its path is represented by the suture between opisthotic and basi-exoccipital (Patterson 1975: 463).

From this brief survey of the occipital fissure in actinopterygians it is evident that a perichondrally-lined fissure is primitive (Gardiner 1973: 106; Patterson 1975: 567). Apart from actinopterygians an occipital fissure is found in acanthodians (*Acanthodes*, Miles 1973a: 66), Palaeozoic selachians (*Xenacanthus*, *Tamiobatis*, Schaeffer 1981), where it is presumed to have been cartilage-filled and uncalcified, early dipnoans (Miles 1977), and rhipidistians (Jarvik 1954: fig. 1; 1972: 64). In all described actinistians the occipital fissure is obliterated, and as in *Polypterus* represented by sutures between bones. In *Laugia* membranous outgrowths from the occipital region further obliterate it (Forey, personal communication).

I have argued elsewhere (Gardiner 1973: 129) that a perichondrally-lined occipital fissure is primitive for osteichthyans (see also Patterson 1975: 466) and is a synapomorphy they share with acanthodians. More detailed examination, however, has convinced me that in *Acanthodes bronni* the fissure is not perichondrally lined.

3. *Vestibular fontanelle*. This lies at the anteroventral corner of the occipital fissure, usually anterior or ventral to the glossopharyngeal foramen, and is open in all known palaeoniscid braincases; it is large in *Pteronisculus* (Nielsen 1942: 48) and *Kentuckia* (Rayner 1951: fig. 7). Though the fontanelle was cartilage-filled in *Mimia* (see particularly Figs 14, 15, 25) the upper part at least is perichondrally lined in *Pteronisculus* (Nielsen 1942: 48), and in *Boreosomus* (Nielsen 1942: 290) the whole fontanelle is perichondrally lined. Apart from these two palaeoniscids no other actinopterygian has been described in which the vestibular fontanelle has a perichondral lining. A vestibular fontanelle is still seen in the pholidopleurid *Australosomus* (Nielsen 1949: 41) and in *Perleidus* (Patterson 1975: 460), but in the latter it is often obliterated in more fully ossified skulls. Within the amioids a large fontanelle persists in some parasemionotids (Patterson 1975: 434), whereas in others such as *Ospia* and some individuals of *Watsonulus* it is again obliterated. A quite large fontanelle persists in pachycormids (Patterson 1975: fig. 106) while in the primitive teleost *Pholidophorus bechei* (Patterson 1975: fig. 56) the fontanelle is as large as in *Mimia*. In some other species of *Pholidophorus* the fontanelle is closed. In Recent teleosts the vestibular fontanelle can often be recognized in the adult neurocranium as an area of membrane or cartilage at the junction of the prootic, basioccipital and exoccipital. Thus it would seem that primitively in actinopterygians the vestibular fontanelle was cartilage-lined and confluent with the cranial fissure.

The vestibular fontanelle clearly corresponds to the basicapsular fenestra of the embryo

(Patterson 1975: 466). In the embryo the basicapsular fenestra is that space between the auditory capsule and the parachordal cartilage, bounded anteriorly by the embryonic connection of the capsule to the parachordals, the anterior basicapsular commissure (de Beer 1937: 399). A long metotic fissure separates the otic capsule from the parachordals posteriorly in both selachians and osteichthyans, and the basicapsular fenestra is eventually closed off posteriorly by the posterior basicapsular commissure, but this often happens quite late in ontogeny: not until the 9.5 mm stage in *Amia* (Pehrson 1922) or the 11 mm stage in *Lepisosteus* (Veit 1911, Hammarberg 1937). Thus, in the palaeoniscids and other primitive actinopterygians, the relationship of the vestibular fontanelle to the occipital fissure resembles that seen in early fish embryos.

A vestibular fontanelle, cartilage-filled in life, is also present in the rhipidistians *Eusthenopteron* (Jarvik 1954: fig. 1) and *Youngolepis* (Chang 1982: fig. 10), and an area of the braincase wall of *Acanthodes* (Miles 1971a: fig. 4.7, Jarvik 1977: fig. 3) anteroventral to the occipital fissure and devoid of perichondral bone possibly included the vestibular fontanelle. Miles (1977: 49) has argued that since the fontanelle is filled with cartilage in most primitive actinopterygians, and can thus close in bone during ontogeny, it is devoid of phylogenetic significance. Hence, though dipnoans lack a fontanelle they do not differ significantly from primitive actinopterygians and *Eusthenopteron* in this respect. However, from the history and occurrence of the vestibular fontanelle I regard the absence of the fontanelle in dipnoans as a derived character, in contrast to its absence in palaeoniscids and *Eusthenopteron*.

The vestibular fontanelle is obliterated in actinistians but persists in tetrapods where it forms the fenestra ovalis of the auditory capsule. A vestibular fontanelle has also been recorded in fossil selachians (*Xenacanthus*, *Tamiodontis*, Schaeffer 1981: figs 5, 21).

From the arguments outlined above for the occipital fissure and from the fact that the vestibular fontanelle is present in selachians, actinopterygians, rhipidistians and tetrapods I conclude that a cartilage-lined fontanelle is a primitive gnathostome character.

4. *Ventral otic fissure.* In the Gogo palaeoniscids *Kansasiella*, *Pteronisculus macropterus* and *Boreosomus*, the ventral otic fissure is separate from the vestibular fontanelle.

In other palaeoniscids such as *Pteronisculus stensioei* (Nielsen 1942: figs 4, 6), *Kentuckia* (Rayner 1951: fig. 9) and 'Ambipoda' (Beltan 1968: fig. 4) the ventral otic fissure passes through the base of the otic region and runs into the vestibular fontanelle; thus the endocranium contains two median ossifications in the adult. However, since the position of the ventral otic fissure in the Gogo palaeoniscids represents the gap between the trabeculae (+ polar cartilages) and parachordals in the embryo (Gardiner 1973: 106) and is in an identical position to the ventral part of the intracranial joint in rhipidistians (*Eusthenopteron* Jarvik 1954; *Glyptolepis* Jarvik 1972) and actinistians (*Latimeria* Millot & Anthony 1958, 1965; *Diplocercides* Bjerring 1972: fig. 3), the anterior position of the fissure must be primitive for osteichthyans (Gardiner 1973: 107). Subsequently in actinopterygian evolution the fissure migrated backwards, as the myodome developed, and became confluent with the vestibular fontanelle and the occipital fissure (Gardiner 1970, 1973: 106; Patterson 1975: 541; Gardiner & Bartram 1977: fig. 8). Bjerring (1978) however, has denied the homology of the intracranial joint with the ventral otic fissure, and Schaeffer & Dalquest (1978) have doubted the migration of the ventral otic fissure in actinopterygians.

In all other actinopterygians, where it is possible to distinguish the two fissures, the ventral otic fissure is a ventral continuation of the occipital fissure, through the vestibular fontanelle. In *Polypterus* the ventral otic fissure persists as a broad tract of cartilage between basisphenoid (= sphenoid) and basioccipital, but in *Australosomus* (Nielsen 1949: fig. 4) it is much narrower and clearly opens into the vestibular fontanelle. Similarly in lightly ossified specimens of *Perleidus* (Patterson 1975: 460) and in *Birgeria* the ventral otic fissure is represented by a large tract of cartilage contiguous with the vestibular fontanelle.

In *Amia* and *Lepisosteus* the fissure is represented by a broad band of cartilage between the basioccipital and prootics. In parasemionotids (Patterson 1975: 434), though often obliterated externally, the ventral otic fissure is visible as a suture on the internal bone surface. The fissure is

also observable in *Lepidotes* (Patterson 1975: 450), young individuals of pachycormids, later pholidophorids and leptolepids (Patterson 1975: 466). In all living teleosts it is represented by the suture or cartilage between the prootics and basioccipital. From the position of the ventral otic fissure in *Mimia* (and perhaps *Polypterus*, see above) it appears that primitively the fissure passed between the basioccipital and basisphenoid (ossifications deduced from Patterson 1975) at least in its most ventral part (Gardiner & Bartram 1977: 230). Subsequently, as a consequence of myodome formation and accompanying rearward migration of the fissure, the prootics replace the basisphenoid as the anterior margin of the ventral otic fissure in later actinopterygians.

Patterson (1975: 466) has shown that in many primitive actinopterygians, such as *Saurichthys*, some specimens of *Perleidus* and parasemionotids, early caturids, *Dapedium*, and early pholidophorids and leptolepids, all forms in which sutures do not persist in the fully ossified braincase, the ventral otic fissure may close completely. This is of interest in relation to the possibility of neurokinesis in actinopterygians. Schaeffer (1968: 216) has argued that where confluence of the ventral otic fissure and occipital fissure has occurred there is the possibility of the two halves of the neurocranium moving relative to one another and that a flexible joint existed in palaeoniscids. I have argued elsewhere (Gardiner 1970: 286) that in primitive palaeoniscids, at least, there was never any neurokinesis, whereas Patterson (1975: 418) has demonstrated that no such kinesis could have occurred in pholidophorids. Patterson (1975, and see above) has also shown how, within almost every actinopterygian group, closure of one part or another of the two fissures has taken place. It would appear that the only possible candidates for neurokinesis are those post-Devonian palaeoniscids such as *Pteronisculus* (Nielsen 1942), *Kentuckia* (Rayner 1951), *Paramblypterus* (Heyler 1969), '*Ambipoda*' (Beltan 1968) and the pholidopleurid *Australosomus* (Nielsen 1949) in which the ventral otic fissure and occipital fissure are continuous and the parasphenoid ends at the ventral otic fissure. But in *Pteronisculus* there are species (*P. macropterus*) in which the two fissures are still separate (Beltan 1968: pl. 2), while in *Australosomus* the configuration of the dermal skull roof (Nielsen 1949: fig. 21) makes neurokinesis highly unlikely. Furthermore, no living cladistian or chondrosteian shows any semblance of neurokinesis. Therefore it is highly unlikely that any actinopterygian ever exhibited neurokinesis (see also Pearson & Westoll 1979: 386).

As stated earlier (p. 204) it is my belief that the ventral otic fissure corresponds to the ventral part of the intracranial joint in actinistians and rhipidistians (Gardiner 1970: 286; Gardiner 1973: 108). Jarvik (1954, 1960, 1968, 1972) and Bjerring (1967, 1973) have insisted that the intracranial joint is a persisting vertebral joint and therefore primitive for gnathostomes. This has led to some disagreement over the exact position of the ventral otic fissure in actinistians and rhipidistians. Jarvik (1954) believed that the more posterior position of the ventral fissure in *Pteronisculus* was primitive and homologized it with a cartilage-filled fissure in an apparently similar position, linking the vestibular fontanelles in *Eusthenopteron*. Bjerring (1971) on the other hand claimed that it was homologous with his 'anterior intraotic joint' and later (Bjerring 1973) insisted that the intracranial joint was not homologous in rhipidistians and actinistians. These arguments have been critically reviewed at length elsewhere (Miles 1975, 1977; Patterson 1975; Gardiner & Bartram 1977; Wiley 1979) and as Miles (1977: 50) succinctly summed them up, 'the best reason for rejecting Jarvik's and Bjerring's conclusions is that they lead to unacceptable phylogenetic results.' No such difficulties arise if we consider a ventral otic fissure as primitive for osteichthyans and the intracranial joint a shared specialization of actinistians and some rhipidistians (see also Rosen *et al.* 1981: 259).

Finally, the condition of the ventral otic fissure in dipnoans is of interest since it closely parallels that of later actinopterygians (Miles 1977: 50). Although there is no myodome in dipnoans, the ventral otic fissure has migrated posteriorly and is covered by a long parasphenoid stem. In the Gogo dipnoans *Griphognathus* and *Chirodipterus* (Miles 1977: figs 13, 17) the ventral otic fissure is already continuous with the occipital fissure, there is no expanded vestibular fontanelle and the median portion of the ventral otic fissure has been obliterated externally, much as in some parasemionotids. I have suggested elsewhere (Gardiner 1973: 108) that early phylogenetic obliteration of this inherent line of weakness in the braincase

floor of dipnoans is related to their specialized feeding habits and to the concomitant fusion of the palatoquadrate and neurocranium. The parasphenoid also grew back to close over the the ventral otic fissure in later actinopterygians and possibly in tetrapods other than ichthyostegids (but see Rosen *et al.* 1981: 259).

5. *Supraoccipital*. This does not occur in *Polypterus* or *Acipenser* or in any fossil or living lepisosteoid, amioid, pachycormid or semionotid (Patterson 1975: 432–450); nevertheless it is characteristic of pholidophorids and teleosts. However, since a supraoccipital may be present in palaeoniscids such as *Mimia* and *Moythomasia*, its absence in amioids, pachycormids and semionotids could be a derived condition. A supraoccipital occurs in actinistians and tetrapods, and the median ossification in the upper margin of the occipital arch of *Eusthenopteron* (Jarvik 1975: fig. 9), immediately behind the posterior dorsal fontanelle, may also represent a supraoccipital.

The presence of a supraoccipital is therefore considered a primitive osteichthyan condition.

6. *Aortic canal*. This is always present in palaeoniscids and is a common feature in other primitive actinopterygians. Patterson (1975: 320) has demonstrated how the point at which the dorsal aorta bifurcated and the aortic ligament originated on the braincase migrated backwards in actinopterygian evolution; he suggested this movement may be correlated with enlargement of the circulus cephalicus (or lengthening of the lateral aortae). This rearward migration of the point of bifurcation of the dorsal aorta presumably resulted in shortening or obliteration of the aortic canal. In other forms where the lateral aortae remain short, such as *Acipenser*, *Polyodon* (Danforth 1912: 442, fig. 15), *Amia* and *Lepisosteus* (Goodrich 1930), backward growth of the parasphenoid may also have caused loss of the aortic canal (Gardiner 1973: 116). A short but distinct canal still exists in some parasemionotids (*Broughia* Stensiö 1932b: 270), the semionotid *Dapedium* (Frost 1913: fig. 1; Gardiner 1960: fig. 38, and in some leptolepids (Patterson 1975: 319). In Recent teleosts an aortic canal has been reported in the notopterid *Xenomystus* (Taverne 1973) but Patterson & Rosen (1977: 129) have shown this to be a neomorph produced in relation to the ear/swimbladder connection. An aortic canal is clearly a primitive feature in actinopterygians.

There is no aortic canal in actinistians, and the canal is also absent in dipnoans and rhipidistians. That the canal should be missing in dipnoans and rhipidistians is not surprising since in both groups there is good evidence to show that the dorsal aorta bifurcated behind the occiput (*Ectosteorhachis* Romer 1937: fig. 1; *Eusthenopteron* Jarvik 1954: fig. 7; *Chirodipterus* Sæve-Söderbergh 1952, Miles 1977: fig. 18; *Neoceratodus* Sewertzoff 1902: 593). Miles (1977: 56) has suggested that absence of the aortic canal in dipnoans is secondary and correlated with backward expansion of the parasphenoid, but it seems more likely to be related to the fact that dipnoans, like primitive tetrapods, have long lateral dorsal aortae (or epibranchial arteries) and this places the point of bifurcation of the aorta behind the occiput. Moreover, expansion of the parasphenoid has not occurred in actinistians or rhipidistians, yet they all lack an aortic canal. Despite there being no aortic canal in dipnoans and no sign of an aortic ligament in Recent dipnoans, Miles (1977: fig. 13) considered a pit on the hind face of the occiput in *Griphognathus*, between the parasphenoid and cranial centrum, to be the site of origin of the aortic ligament. He (1977: 56) further suggested that a similar notch in the back of the parasphenoid in *Birgeria* (Nielsen 1949: fig. 62) was for the aortic ligament. In actinopterygians where there is any evidence of an aortic ligament, even in Recent clupeoids, salmonoids and cyprinoids, the point of attachment is always to the basioccipital and not, as in *Griphognathus*, to the base of the cranial centrum. Moreover, it is difficult to believe that *Birgeria* differs from all other described palaeoniscids, *Polypterus* and chondrosteans in having the bifurcation of the dorsal aorta behind the occiput, particularly since a similar notch in the back of the parasphenoid is to be seen in *Polypterus*, *Saurichthys* (Stensiö 1925) and *Chondrosteus* (RSM 1887.15.2).

Outside osteichthyans an aortic ligament is said to have been present in *Acanthodes* (Miles 1973a: fig. 5), but the only record of an aortic canal other than in actinopterygians is in the holocephalan *Helodus* (Moy-Thomas 1936: fig. 4). In all living selachians the paired lateral

aortae are comparatively shorter than in *Polypterus*, *Acipenser*, *Amia* and *Lepisosteus*, and the dorsal aorta bifurcates behind or just at the level of the occiput. The lateral aortae are often enclosed in paired canals in primitive selachians such as *Cladodus* (Gross 1937: fig. 5), *Cladoselache* (Harris 1938: 9), *Tamiodontis* (Romer 1964) and xenacanth (Schaeffer 1981: fig. 6); they are similarly enclosed in the living carcharhinoid *Dirrhizodon* (Compagno 1973: 19). In other fossil selachians such as *Hybodus* (Maisey 1983) the lateral aortae lay in well-marked grooves beneath the occipital region much as in *Megalichthys*. In placoderms such as *Wildebeekia* (Young 1978) there are long paired grooves on the occipital region which must have housed the lateral aortae, but in *Brindabellaspis* (Young 1980: fig. 7) the lateral aortae pass through separate canals as in *Cladodus*.

A median aortic canal is therefore present only in actinopterygians and holocephalans, and it is not possible to decide whether it has arisen independently in the two groups or is a primitive gnathostome character.

7. *Canal for abducens nerve*. Primitively in actinopterygians the abducens nerve passed through the basioccipital and entered the orbit through the corner of the prootic. In *Latimeria* (Millot & Anthony 1958) the abducens is said to pass down through the floor of the saccular cavity without piercing any ossification. This course is not surprising since the basioccipital is small and confined to the posterior end of the neurocranium. However, in the rhipidistian *Eusthenopteron* Jarvik (1972: fig. 93) has restored the neurocranium with a foramen for the abducens in the edge of the ossification lateral to the notochord. This foramen is in the prootic (deduced from a similar ossification in actinopterygians and *Latimeria*), but in *Eusthenopteron*, as in *Latimeria*, the basioccipital does not extend ventrally beneath the anterior portion of the notochord. The path of the abducens in dipnoans is difficult to follow; for example, in the development of *Neoceratodus* the abducens is intimately connected with the roots of the facial and trigeminal nerves (Fox 1965: 505). Nevertheless this nerve never passes through the prootic bridge as in later actinopterygians; in the Devonian *Chirodipterus* (Miles 1977: figs 17, 21) it is presumed to pass laterally with V and VII through the prootic area. In the development of amphibians such as *Ambystoma* (Goodrich 1911) the abducens nerve still pierces the anterior parachordal (so called because the parachordal is restricted to the extreme anterior end of the notochord) to emerge on the ventral surface of the skull.

I conclude that in osteichthyans the abducens nerve primitively passed through the basioccipital.

8. *Zygale plates*. In primitive actinopterygians such as *Mimia* paired zygale plates are found in the roof of the notochordal canal. Similar plates are also present in *Moythomasia*, but in other palaeoniscids such as *Pteroniscus* the zygale plate is median and unpaired. In actinopterygians zygale plates are found only in palaeoniscids. They appear to be present in all actinistians. In *Nesiodon* (Bjerring 1971: 194) the zygals are said to be paired, but in *Latimeria* (Millot & Anthony 1958: pl. 17) there is a median, bilobed plate. In rhipidistians paired zygals have been reported in *Eusthenopteron* (Bjerring 1971: 192) but in *Glyptolepis* (Jarvik 1972: 68) there is a median plate as in *Latimeria*.

From this distribution we may conclude that paired zygale plates are a primitive osteichthyan feature. It is easy to see how, with increase in size of the myodome and concomitant regression of the notochordal canal, they have been lost in later actinopterygians. The zygals appear to play an important part in the intracranial joint in *Latimeria* and some rhipidistians; they are missing in dipnoans and tetrapods.

9. *Occipital artery*. Primitively, this appears to be related to the second permanent myomere, since in both *Mimia* and *Moythomasia* the foramen for the artery arises between the ridges for the insertion of the first and second intermuscular septa. This direct relationship, also seen in *Amia*, is recognizable in any other actinopterygian, but in the rhipidistian *Ectosteorhynchus* (Romer 1937: fig. 2) the foramen for the occipital artery opens in the line of the ridge for the second intermuscular septum and presumably belongs to the second permanent segment, not

the third as suggested by Romer (1937: 8). Support for this view can be obtained from one specimen of *Mimia* (BMNH P.54501) in which that part of the basioccipital around the aortic canal and notochord projects posteriorly for some distance as it does in *Ectosteorachis*. Furthermore, in the development of *Polypterus* Allis (1922: 208) has demonstrated how the basioccipital portion of the basi-exoccipital can project posteriorly beyond its exoccipital portion to a distance equal to about half that of the first free vertebra and still be part of the segment anterior to it (that incorporating the ventral root of the second occipital nerve). Elsewhere an occipital artery has been described in *Eusthenopteron* where it is also presumably related to the second permanent occipital segment (Jarvik 1975: fig. 8). A similar dorsolaterally-directed canal has also been described in Devonian dipnoans (Säve-Söderbergh 1952: figs 1, 8; Miles 1977: figs 11, 15, 23), but its relationships with neighbouring foramina is not clear. The course of the occipital artery has been described in *Neoceratodus* (Spencer 1893: 10) and an artery in a similar position exists in urodeles (Drüner 1901) and anurans (Gaupp 1899). In placoderms such as *Brindabellaspis* (Young 1980: fig. 7) the occipital artery passed into the cranial cavity in the vicinity of the first occipital nerve, and then appears to have run backwards through the occiput. Finally in *Acanthodes* (Miles 1973a: fig. 3) the foramen for the occipital artery again appears to be related to the second occipital segment since it lies in front of the opening for the second occipital nerve (first occipital, see below).

The primitive course of the occipital artery after leaving its canal in the basioccipital is less certain. In *Amia* (Allis 1897: 706) it runs up over the lateral surface of the basioccipital and exoccipital onto the dorsal surface of the occiput, where it sends branches to all occipital myomeres. In *Polypterus*, although there is no occipital artery as such, the first intervertebral artery apparently takes over its function. In a 75 mm larva, Allis (1922: 207) has shown how the intervertebral artery divides into two and the anterior branch passes into a canal in the basioccipital. From thence one part of it passes into the cranial cavity through the second occipital nerve canal and the other continues up towards the second intermuscular septum. The posterior branch also enters the cranial cavity, but through the canal for the ventral root of the first spinal nerve. Unfortunately, in other living osteichthyans the occipital artery either does not groove the surface or does not enter the occiput, consequently there is no model on which to base the distribution of the various branches. Nevertheless, a system of grooves for the branches of this artery has been recognized in the rhipidistian *Eusthenopteron* (Bjerring 1971: fig. 18; Jarvik 1975: fig. 9).

From the evidence given above for both *Mimia* and *Moythomasia* the canal which enters the anterior floor of the foramen magnum after running through the exoccipital at right angles to the long axis of the neurocranium must have carried a branch of the occipital artery and not an occipital nerve. If this is so then the canal in a corresponding position in *Kansasiella* (Poplin 1974: figs 24, 25) must also have served for a branch of the occipital artery. It follows that a canal with identical relationships and running at right angles to the long axis of the brain in the rhipidistian *Ectosteorhachis* (Romer 1937: fig. 9) must also have served for a branch of the occipital artery, not the first occipital nerve as suggested by Romer (1937: 8). It should be noted that occipital nerves normally run obliquely backwards to their points of exit. It also seems likely that in *Acanthodes* (Miles 1973a: fig. 2) the foramen lying in the groove for the occipital artery transmitted a branch of that artery rather than the first occipital nerve.

10. *Segmental structure of occiput.* In view of the variable composition of the occipital region in Recent fishes and the loss of somites from the metotic series during development, determination of the primitive number of adult occipital myomeres is difficult. For example, among actinopterygians *Polypterus* has incorporated one centrum into its braincase, *Amia* two, *Lepisosteus* three, and *Acipenser* up to eight; among dipnoans *Neoceratodus* has added three.

In the Gogo palaeoniscids there must have been at least two permanent myomeres, more probably three, judged from the position of the two intermuscular septa and the single occipital nerve canal. A similar condition existed in pholidophorids and leptolepids (Patterson 1975: 318). In all these forms the first myomere is characterized by the absence of any canal for an occipital nerve. From this evidence I conclude that the ancestral condition for actinopterygians

is a single occipital nerve canal (which carried a ventral root only) related to the second permanent myomere.

In *Latimeria* (Millot & Anthony 1958) both the basioccipital and the paired exoccipitals are much reduced; nevertheless, together with the 'supraoccipital' these ossifications must represent the first and only occipital sclerotomes, since they are associated with the first trunk muscle. There is no corresponding occipital nerve; instead the associated nerve leaves the foramen magnum posterior to this segment. Other Recent bony fishes in which the first occipital myomere has either no related ventral nerve root, or if it does, whose nerve exists in a more

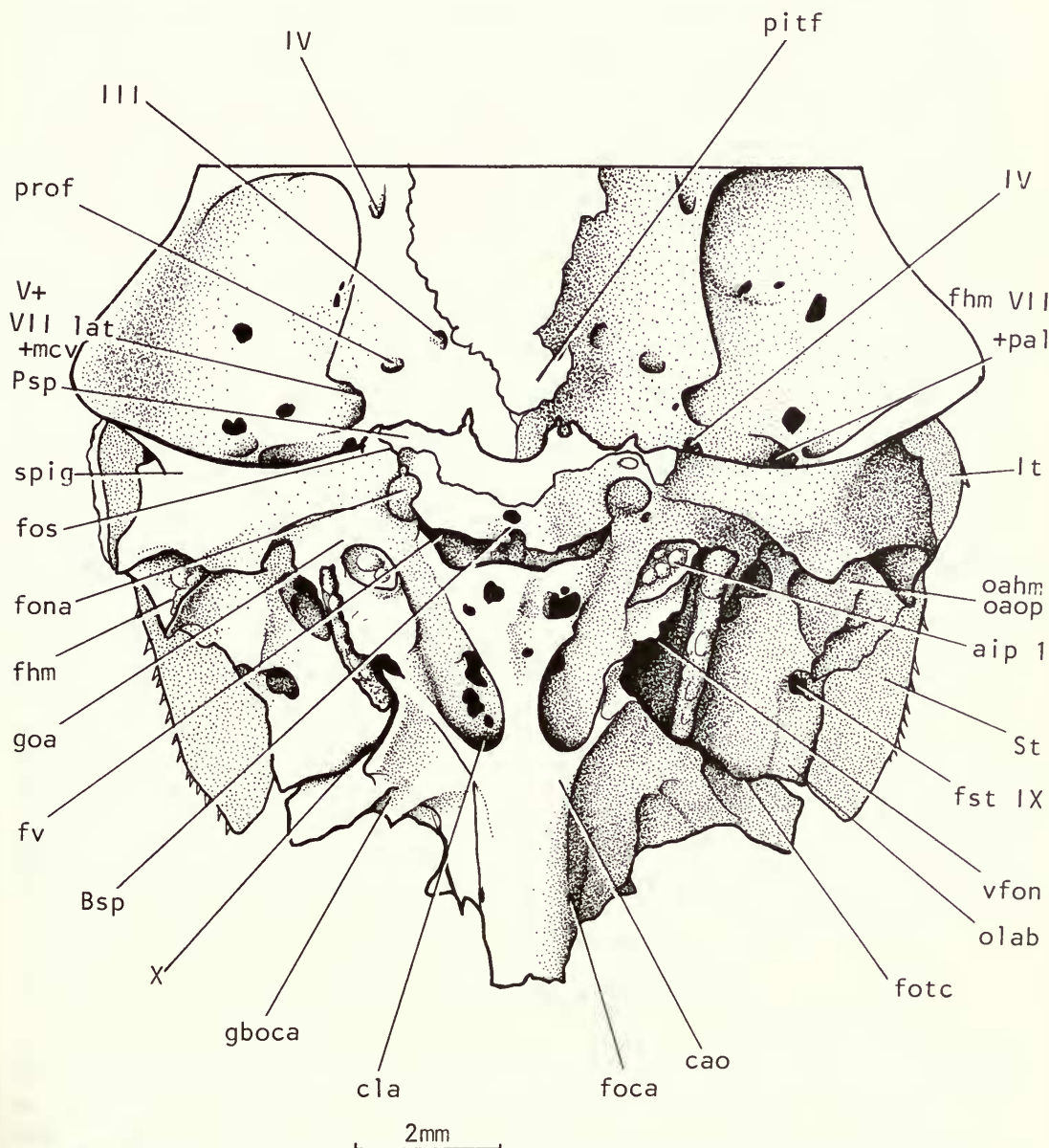


Fig. 15 *Mimia toombsi* Gardiner & Bartram. Occipital, otic and orbitotemporal regions of neurocranium and attached dermal bones in ventral view, from BMNH P.56483. Anterior regions of parasphenoid and basisphenoid missing.

posterior segment, include *Amia* (Allis 1897: 725), *Polypterus* (Allis 1922: 207), *Lepisosteus* (Schreiner 1902), and *Lepidosiren* (Bridge 1898). Furthermore, in the development of the amphibian *Ambystoma* (Goodrich 1911) the first permanent myomere never has a ventral root. On the other hand *Cryptobranchus* (de Beer 1927) is said to be unique among living amphibians in possessing one pair of occipital foramina, but there is evidence of two segments in this animal.

In *Ectosteorhachis* (Romer 1937), *Rhizodopsis*, *Eusthenopteron* (Jarvik 1975) and *Youngolepis* (Chang 1982) there is evidence from the imprint of the intermuscular septa and the course of the occipital artery of three occipital myomeres, as in *Mimia*. Two pairs of foramina have also been described in the occiput of all four genera. The posterior pair (posterior spino-occipital nerve canals of Jarvik 1975) corresponds to the occipital nerve (ventral root) foramina of *Mimia*, while the anterior pair (anterior spino-occipital nerve canals of Jarvik 1975) occupies a similar position to foramina I attribute to branches of the occipital artery in *Moythomasia* and *Mimia*.

In *Griphognathus* and *Chirodipterus* (Miles 1977) the occipital foramen is followed posteriorly by three pairs of spino-occipital nerve foramina, and in *Holodipterus*, *Dipterus* and *Conchopoma* (Schultze 1975) by at least two pairs of spino-occipital nerve foramina. The skull of *Neoceratodus* (Fox 1965) includes three occipital arches (one occipital and two spino-occipital), that of *Protopterus* (de Beer 1937) two, and *Lepidosiren* one (Agar 1906). In *Protopterus* the occiput is pierced by a single pair of occipital nerves and in *Neoceratodus* the occiput encloses two pairs of spino-occipital nerves.

In many selachians the occipital nerves leave either through the vagus canal or behind the condyles. Nevertheless, in *Scyllium* (de Beer 1937), where the occiput is believed to comprise three segments, the occipital arch is pierced by a single pair of occipital nerves. In *Xenacanthus*, *Tamiobatis* (Schaeffer 1981) and *Hybodus* (BMNH P.50869) the occipital region is pierced by at least three (four in *Hybodus*) pairs of nerve foramina, but foramina are apparently wanting in *Cladoselache*, *Cobelodus* and 'Cladodus' (Schaeffer 1981).

In placoderms there are invariably several pairs of occipital nerve foramina; up to seven pairs of spino-occipital nerves have been described in *Buchanosteus* (Young 1979), five pairs in *Brindabellaspis* and three pairs in *Ctenurella* (Miles & Young 1977).

Finally in *Acanthodes* the basioccipital is almost as extensive as in *Mimia* and incorporates the foramen for the occipital artery, whereas the 'lateral occipital' includes the foramen for the occipital nerve as well as a more anterior foramen (Miles 1973a: fig. 2, on1) for a branch of the occipital artery.

From this brief survey I conclude that the first myomere of osteichthyans is characterized by the absence of an occipital nerve.

11. *Longitudinal intervertebral ligament.* The presence of this is a primitive feature for gnathostomes (Goodrich 1930: 21), and in later actinopterygians such as parasemionotids and semionotids the ligament terminated in a deep, cartilage-lined pit in the exoccipital region above the foramen magnum. A comparable pit in the same region has been described in the Devonian dipnoans *Griphognathus* and *Chirodipterus* (Miles 1977: figs 12, 16), and an unossified area immediately above the foramen magnum in *Eusthenopteron* (Jarvik 1975: fig. 10) presumably served the same function.

Otic and orbitotemporal regions

Review of ossification centres

The otic and orbitotemporal regions of the braincase consist of a single ossification which shows few sutures, apart from the otico-sphenoid fissure. Several of the more lightly ossified specimens of *Mimia* (BMNH P.56495, P.56496) and *Moythomasia* (BMNH P.56480) do, however, show partial gaps in the perichondral lining of the internal surface of the neurocranium, which give some indication of the internal extent of the individual ossifications. The external extent of these ossifications is occasionally marked by faint sutures and by the more obvious fissures (ventral otic fissure, otico-sphenoid fissure; fv, fos, Fig. 22). From such specimens it is possible (by

comparison with *Perleidus*, parasemionotids and pholidophorids) to estimate the extent of the individual bones with confidence. Thus in *Mimia* and *Moythomasia* it appears that the prootic ossifies around a centre in the lateral commissure and occupies only a small part of the outer lateral wall of the braincase and the posteroventral corner of the orbit, but probably includes the trigeminal and facial foramina. Internally the prootic forms the anterolateral wall of the otolith chamber and the ampullary chambers of the anterior and external semicircular canals. Dorsally the prootic forms the anteromedial portion of the lateral cranial canal. I conclude that the prootic forms a smaller part of the braincase than in parasemionotids and a considerably smaller part than in pholidophorids (Patterson 1975). This discrepancy may be directly related to the absence of a myodome in the Gogo palaeoniscids, since in pholidophorids, leptolepids and Recent teleosts where the myodome is extensive the prootic is proportionally larger. The prootic is large in fossil actinistians and *Latimeria* (Millot & Anthony 1958) where the bone extends posteroventrally as far as the ventral fissure and posterolaterally to the hyomandibular facet.

The prootic is small in *Acipenser* and occupies only the posteroventral corner of the orbit. In *Polypterus* the prootic is a transient ossification only seen in embryos (Pehrson 1947: 405), where it forms a small perichondral thickening around the posterior margin of the trigeminal foramen. Elsewhere within the palaeoniscids a prootic is absent from *Birgeria* (Nielsen 1949). In all these forms the ascending process of the parasphenoid is long and complex and covers that lateral area of the neurocranium normally occupied by the prootic. A prootic is not obviously present in *Acanthodes* (see for example Miles 1973a: fig. 2; Jarvik 1977: fig. 3). The prootic appears to have been a small ossification (smaller than the opisthotic) in primitive actinopterygians. Its increase in size and importance in later halecomorphs and teleosts is presumed to be related to myodome formation, whereas its large size in actinistians may be related to the absence of a sphenotic.

A separate stout sphenotic ossifies from a centre in the postorbital process. In *Mimia* it is presumed to extend posteriorly as far as the hyomandibular facet which marks the junction between it and the opisthotic. A wide groove on the face of the postorbital process housed the spiracle which opened dorsally on the skull roof. An endoskeletal spiracular canal is absent, but occasionally a pair of processes partially delimit the top of the spiracular groove (Fig. 14; Gardiner 1973: fig. 5). Similar processes in *Moythomasia* (Fig. 28) may join to form a complete bar (spic, Figs 7, 30). An endoskeletal spiracular canal is characteristic of most palaeoniscids (*Pteronisculus*, *Boreosomus*, *Kentuckia*, *Kansasiella*, *Birgeria* etc.), *Perleidus* (Stensiö 1932b: fig. 59), *Australosomus* (Nielsen 1949), many fossil halecostomes including *Pholidophorus* (Patterson 1975: 399) and all extant chondrosteans and holosteans; it is absent in *Polypterus*. Within primitive actinopterygians a separate sphenotic has been described in *Cosmoptychius* (Watson 1928; Schaeffer 1971), *Perleidus* (Patterson 1975), *Birgeria* and *Polypterus* and is universally present in halecomorphs and teleosts. A similar ossification of the postorbital process in *Acanthodes* (Miles 1973a: fig. 1; Jarvik 1977: fig. 3) may also be a sphenotic since, as in primitive actinopterygians, it forms the anterior margin of the hyomandibular facet; the suggestion by Jarvik (1977: 207) that the head of the hyomandibula articulated with the middle of the otic ossification is considered unlikely since in ossified neurocrania the hyomandibular facet always lies at the junction of two or more ossifications. An ossified postorbital process is also present in placoderms (*Buchanosteus* Young 1980) and a tesserate postorbital process is a prominent feature of most chondrichthyans. The sphenotic is apparently missing from those actinistians in which separate ossifications have been described (*Wimania* Stensiö 1921, 1925; *Macropoma*, *Whiteia* Beltan 1968: 114; *Rhabdoderma* Forey 1981; *Latimeria* Millot & Anthony 1958) and a single ossification occupies the area of the basisphenoid, pterosphenoid and sphenotic. This ossification also includes the postorbital process (antotic process of other authors). The postorbital process is missing in *Ectosteorhachis* and *Rhizodopsis* whereas in *Eusthenopteron*, *Holoptychius* and *Glyptolepis* (Jarvik 1972: figs 20, 21) it is represented by the supratrigygoid process.

The anterior internal limits of the opisthotic can be estimated from *Mimia* (BMNH P.56496). Its external limits can be confirmed partly from *Cosmoptychius* (Schaeffer 1971: fig. 8, ot), where a separate opisthotic forms the anterior wall of the vagus canal and includes the canal for

the glossopharyngeal nerve and a groove for its supratemporal branch (Watson 1928: 49), and partly from *Polypterus* where the bone is very large.

The opisthotic in *Mimia*, *Cosmoptychius* (Schaeffer 1971: fig. 8A), *Pteronisculus* (Nielsen 1942: 16; fig. 3) and *Perleidus* (Patterson 1975: fig. 115) has a posteroventral tongue and includes the lower portion of the posterior semicircular canal as well as the external semicircular canal. The centre of ossification in *Mimia* (and *Moythomasia*) is around the ampulla of the posterior semicircular canal and is indicated by the downwardly projecting parampullary process (pamp, Fig. 6) but it extends anteriorly to meet the sphenotic, thereby forming the posterior margin of the hyomandibular facet. The hyomandibular facet also marks the junction between the opisthotic and sphenotic in *Pteronisculus* and *Perleidus*. Anterodorsally the opisthotic provides a large facet for the origin of much of the constrictor hyoideus dorsalis (oahm + oaop, Figs 1, 4, 5, 13) muscle. In the 75 mm *Polypterus* described by Allis (1922: 219) the opisthotic begins to form around the projecting hind end of the otic capsule; that is, around the base of the posterior semicircular canal. In the large specimen of *Polyodon* described by Bridge (1878) the opisthotic is represented by a thin perichondral ossification superficial to the ampulla of the posterior semicircular canal. In *Acipenser* it forms in a comparable position between the foramina of the glossopharyngeal and vagus nerves (Holmgren & Stensiö 1936: fig. 336). The opisthotic is absent in semionotids, *Amia* and *Lepisosteus* as well as leptolepids and more advanced teleosts.

There is a well-marked parampullary process in actinistians (*Nesides*, Bjerring 1977: fig. 23; *Latimeria*, Millot & Anthony 1958) and in several forms (*Macropoma*, *Laugia*, *Wimania*, Stensiö 1921) this is borne on a discrete, small ossification which, by comparison with actinopterygians, must be an opisthotic. The probable centre of an opisthotic in rhipidistians is indicated by the postotical process in *Eusthenopteron* (Jarvik 1954: figs 1, 21) and the 'paroccipital process' in *Ectosteorhachis* (Romer 1937: fig. 1). In both cases the centre of ossification is inferred to lie lateral to the base of the posterior semicircular canal. In actinistians the centre of ossification appears to lie somewhat more anteriorly, around an opening in the wall of the labyrinth cavity (Jarvik 1954: fig. 4, fplab) just in front of the parampullary process. The opisthotic seems to be large in early actinistians and rhipidistians. In *Nesides* (Jarvik 1954: fig. 4; Bjerring 1977: fig. 23) and *Rhabdoderma* (Forey 1981: fig. 1) the opisthotic forms most of the lateral wall of the braincase from the vagus foramen to the hyomandibular facet (both dorsal and ventral parts).

The remaining ossification in the otic region is the pterotic. The extent of this can be inferred partly by comparison with *Perleidus*, where the pterotic is quite small and occupies the posterodorsal corner of the otic capsule (Patterson 1975: fig. 115), and partly from the radiating structure of the bone which is recognizable in several specimens. From this evidence the centre of ossification of the pterotic may be estimated as lying within a dorsolateral prominence in the posterior otic region which presumably served for the origin of the posterior part of the constrictor hyoideus dorsalis (oaop, Figs 4, 5, 6, 13). The constrictor hyoideus dorsalis also originates on the upper outer corner of the otic region of the skull in Recent chondrichthyans such as *Heptanchus*, *Squalus* and *Galeus*. The pterotic is missing in *Birgeria*, *Polypterus* and *Acipenser*; in *Polypterus* the posterior part of the constrictor hyoideus (the adductor opercularis) originates on the opisthotic. The pterotic is proportionally much larger in *Pholidophorus* than in *Mimia* and forms the greater part of the subtemporal and post-temporal fossae but, as in *Mimia*, the centre of ossification is at the posterolateral shoulder of the otic capsule (Patterson 1975: fig. 75), just posterior to the foramen for the supratemporal branch of the glossopharyngeal nerve. In leptolepids and advanced teleosts the pterotic is much reduced, probably as a result of the closure of the cranial fissure (Patterson 1975: 380), its centre of ossification being located along the external semicircular canal.

In *Amia*, *Lepisosteus* and *Lepidotes* there is only one bone in the posterodorsal region of the skull; this may be interpreted as either an epioccipital or a pterotic. Patterson (1975: 443) believes that in *Amia* this so-called 'epiotic' probably represents an epioccipital which has extended forwards following the loss of the pterotic. Since the pterotic primitively appears to have served for the origin of the posterior part of the constrictor hyoideus dorsalis and this muscle (adductor opercularis) partly originates on the intercalar in *Amia* it is reasonable to suppose that the remaining ossification is the epioccipital (associated as it is only with trunk

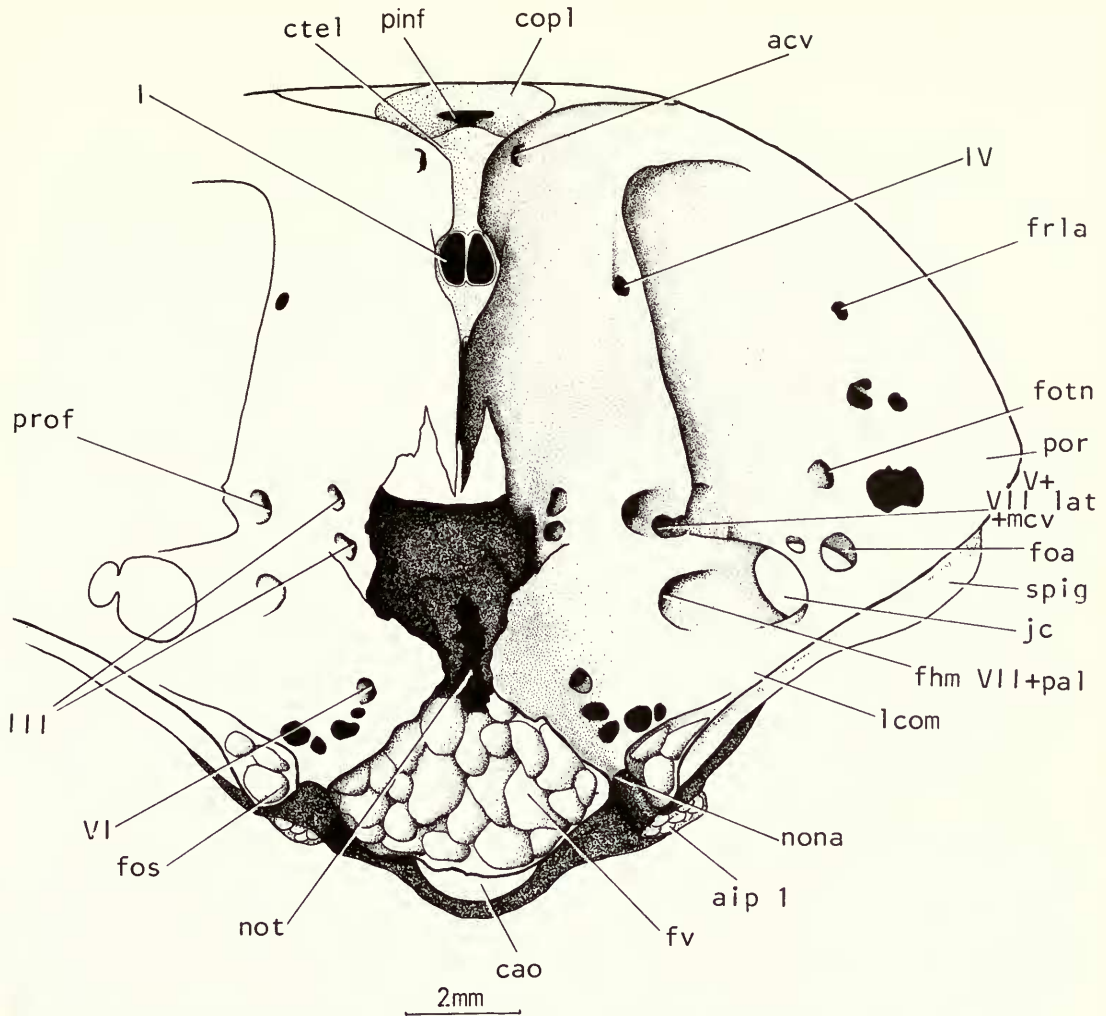


Fig. 16 *Mimia toombsi* Gardiner & Bartram. Otic and orbitotemporal regions of neurocranium in anterior view, as if cut through the middle of the orbit, from BMNH P.53259.

musculature). Patterson (1975: 453) further concluded that in *Lepidotes* this bone represents the pterotic because it includes a blind pit which resembles a dorsolateral expansion of the cranial cavity in the palaeoniscid *Boreosomus* (Nielsen 1942: fig. 66, lv). In *Lepisosteus* it is also likely to be the pterotic since the adductor opercularis is attached to the lateral surface of this bone.

In *Acanthodes* (Miles 1973a: fig. 2, swpamp) a distinct boss, on the braincase wall below the jugular canal and the foramen for the glossopharyngeal nerve, housed the posterior ampulla (but see Jarvik 1977: fig. 3 where a similar swelling lies above the jugular canal). The ridge above this ampullary boss delimits the jugular groove and appears to be the centre of ossification of the otic capsule and presumably also served for the origin of the constrictor hyoideus dorsalis. The centre of ossification of the capsule is more dorsal than the opisthotic in *Mimia* and this together with the presumed muscle origin suggests that the ossification is better homologized with the pterotic than with the opisthotic.

The whole orbital region of the Gogo palaeoniscids, apart from the basiptyergoid process, is ossified as a perichondral shell penetrated by perichondrally-lined canals for nerves and blood vessels. Presumably there were three pairs of ossifications, basisphenoid, pterosphenoid and

orbitosphenoid, as in *Amia* and many teleosts. A separate pterosphenoid has been described in *Pteronisculus* (Nielsen 1942: 90). The basisphenoid is an extensive ossification and its paired nature can be seen in *Mimia* (BMNH P.56483, Fig. 15). Posteriorly it consists of a vertical pillar which flares dorsally into a pair of dorsolaterally-directed arms which join the orbital surface just beneath the oculomotor foramen to form the dorsum sellae (Gardiner & Bartram 1977: 230). Beneath the bridge the junction of the basioccipital with the basisphenoid is marked by the ventral otic fissure. The basisphenoid extends anteriorly for a short distance beneath the orbit to the level of the optic fenestra. The basisphenoid also appears to be paired in *Pteronisculus* (Nielsen 1942: fig. 2) and its centres of ossification are inferred to lie on either side of the vertical pillar, as in *Mimia*. It has been argued elsewhere (Gardiner & Bartram 1977: 237) that the cup-shaped depressions on the basisphenoid pillar in *Mimia* were the points of origin of at least three of the recti muscles. In *Polypterus* (Allis 1922: 252) three of the recti muscles originate (by a short tendinous stalk) on the basisphenoid near its ventral edge and immediately posterior to the optic foramen (as in selachians). The fourth muscle (internal rectus) has its origin slightly more anteriorly, still on the basisphenoid, but anterior to the optic foramen. During development the basisphenoid of *Polypterus* arises from paired perichondral lamellae between the optic and oculomotor foramina. Thus its centre of ossification lies at the point of insertion of the rectus muscles. In other primitive fossil actinopterygians where separate ossifications have been recognized the basisphenoid is only clearly delimited in *Perleidus* (Patterson 1975: 457), and even here it is fused with the prootics.

The basisphenoid in *Pholidophorus bechei* (Patterson 1975: 381) not only forms the pillar but also extends ventrally to form the endochondral floor of the orbit. In later pholidophorids this ventral part is less thoroughly ossified while in leptolepids and advanced teleosts all that remains is a slender pedicel consisting mainly of membrane bone. In most halecomorphs the basisphenoid is a median bone forming little more than the pedicel, as in later pholidophorids. In *Amia*, however, the basisphenoid is a small paired ossification which ossifies late in the transverse 'bolster' in front of the floor of the myodome. Thus, the centre of ossification of the basisphenoid is ventrolateral to that in *Mimia*, *Polypterus* and teleosts. Since three of the rectus muscles originate on this transverse 'bolster' in *Amia* the concomitant shift in ossification centre is hardly surprising. The basisphenoid in pachycormids is not very different from that in *Pholidophorus*, while within the semionotids the basisphenoid of *Lepidotes* is stout and median, and confined to the posteroventral corner of the orbit. In *Lepisosteus* there is no basisphenoid, the rectus muscles originating on the floor of the orbit, lateral to the interorbital septum. Although the shape of the 'basisphenoid' in actinistians suggests that it arises from paired centres, it is never paired either in fossil material or in the embryo (Forey, personal communication). The basisphenoid in *Acanthodes* (Miles 1973a: figs 8, 9) is also a large, unpaired ossification, but is similar in size and shape to that seen in *Mimia*. Its centre of ossification is inferred to lie at the base of the basisphenoid pillar.

That a separate pterosphenoid was present in the orbit of *Mimia* can be deduced from the presence of a distinct ridge running upwards from the trigeminal foramen to the roof of the orbit (Figs 16, 17, 20), and from the presence of a pedicel over the trigeminal and facial foramina in *Moythomasia* (Figs 29, 30). The ridge presumably represents the centre of ossification of the pterosphenoid. The limits of the pterosphenoid can be determined with a fair degree of confidence from estimates of distances between neighbouring ossification centres. From this type of analysis the pterosphenoid appears to occupy well over half of the posterior orbital surface. It extends laterally to just beyond the foramen for the otic nerve, where it meets the sphenotic (junction often marked by a series of fenestrae), and ventrally to just above the trigeminal and facial foramina, where it meets the prootic. It extends anteroventrally to just below the oculomotor foramen where it meets the basisphenoid. Together with the orbitosphenoid the pterosphenoid forms a complete interorbital septum (Fig. 13). Thus the pterosphenoid is possibly a large ossification as in other palaeoniscids and contributes to much of the posterior orbital surface.

A small paired pterosphenoid is found in *Acipenser* but it is absent in *Polypterus*. The pterosphenoid is large in halecomorphs ('*Aspidorhynchus*', Patterson 1975: figs 99, 101;

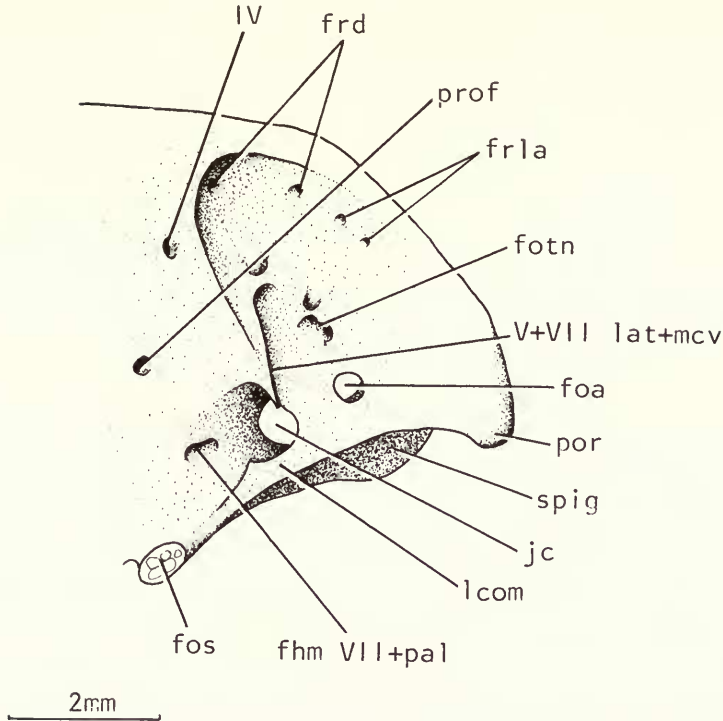


Fig. 17 *Mimia toombsi* Gardiner & Bartram. Left orbitotemporal region of neurocranium in anterior view, from BMNH P.56504.

Macrepistius, Schaeffer 1971: figs 3, 4), semionotids (*Lepidotes*, Patterson 1975: figs 108, 109), pachycormids (*Pachycormus*, Patterson 1975: fig. 106) and pholidophorids (*Pholidophorus*, Patterson 1975: 382). Therefore it seems likely that primitively in actinopterygians the pterosphenoid was an important constituent of the posterodorsal orbital surface. A similar, large dorsal perichondral ossification in the orbit of *Acanthodes* (Miles 1973a: fig. 4; Jarvik 1977: fig. 2) may have included an ossification centre homologous with that of actinopterygians.

In actinistians (*Rhabdoderma* Forey 1981: fig. 1; *Latimeria* Millot & Anthony 1958) there is a single ossification centre in front of the prootic. This ossification fills the area occupied by the basisphenoid, pterosphenoid and possibly the sphenotic in actinopterygians, and also bears the postorbital process (= antotic process). The postorbital process is stout and provides an articulation for the dorsal surface of the palate. In *Acanthodes* (Miles 1973a: figs 2, 15) and some rhipidistians such as *Eusthenopteron* and *Holoptychius* (Jarvik 1954, 1972) the postorbital ossification also bears an articulatory facet for the palate.

Mimia toombsi

The otic region of the neurocranium is separated from the occipital ossification by the posterior dorsal fontanelle dorsally and the occipital fissure laterally, but ventrally the two regions pass into one another without any distinct boundary. The posterior face of the otic region is lined with perichondral bone from the vestibular fontanelle upwards, thus the subvaginal portion of the fissure is open (Fig. 25) as in *Pteronisculus*, *Kansasiella* and some individuals of *Pholidophorus bechei* (Patterson 1975: 232). The perichondral lining is interrupted at the level of the lateral cranial canal (plcc, Figs 11, 12) but otherwise extends dorsomedially to the posterior dorsal fontanelle. Two notches near the posterior margin of the opening of the cranial cavity lead into a pair of shallow, ventrolaterally-directed grooves. The more dorsal groove is the broader and contained the posterior cerebral vein (gpcv, Fig. 11) and a small foramen within the groove

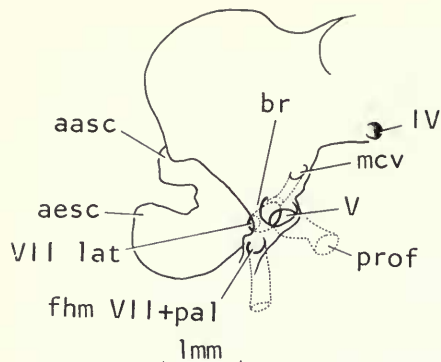


Fig. 18 *Mimia toombsi* Gardiner & Bartram. Internal, medial view of left utricular recess, trigeminal and facial foramina, from BMNH P.56504. Intramural passages indicated by broken lines.

(fapcv, Fig. 11) must have transmitted a small vein into the ampullary cavity of the posterior semicircular canal as in *Pholidophorus bechei* (Patterson 1975: fig. 59). The lower groove was occupied by the vagus nerve, while a large foramen near its lateral limit (gph.X, Fig. 11) which leads out anterolaterally onto the surface of the otic region served for the passage of the pharyngeal branch of the vagus. In other specimens of *Mimia* (cf. BMNH P.56501, Fig. 4) the pharyngeal branch merely notched the end of the vagal canal. A further notch (gst.X, Fig. 11) in the posterolateral margin of the dorsal groove marks the passage of the supratemporal branch of the vagus onto the lateral otic wall.

Below the vagus groove the posterior face of the otic region turns forwards and the perichondral lining gives way to a cartilage-filled vestibular fontanelle (vfon, Fig. 13) as in *Pteronisculus* and other palaeoniscids. The dorsal surface of the otic (Fig. 12) and orbitotemporal regions (Figs 33, 34) is complete and the only opening is the pineal foramen (Pl. 1; pinf, Fig. 33). There is no anterior dorsal fontanelle, in contrast to *Polypterus*, *Pteronisculus* (Nielsen 1942: fig. 7), *Kansasiella* (Poplin 1974: fig. 12), *Kentuckia* (Rayner 1951: fig. 6) and *Pholidophorus* (Patterson 1975: fig. 60). There is also no fossa bridgei and the recurrent lateralis branch of the facial nerve appears to have emerged onto the roof of the otic region just behind the hyomandibular facet and beneath the rim of the intertemporal (frla₂, Figs 6, 11). The dorsal limit of the spiracular groove (spig, Fig. 13) lies in front of the hyomandibular facet, posterior to the postorbital process (por) and the otic nerve (fotn, Figs 12, 13) emerged through its medial wall. In *Kansasiella* (Poplin 1974: fig. 12) and *Pteronisculus* (Nielsen 1942: fig. 12) the otic nerve passed into the spiracular canal. There are two further foramina in the posterior face of the otic region. The more lateral, smaller foramen leads into the lateral cranial canal (fv, Fig. 11); the more medial foramen (dend, Fig. 11) housed the blind-ending endolymphatic duct. From it a gutter runs down towards the cavity occupied by the sinus superior (Fig. 26). There is a recess in the roof of the otic region (rsoc, Fig. 11) which marks the anterior limit of the posterior fontanelle. In *Pholidophorus bechei* (Patterson 1975: fig. 65) the membranous extension of the supraoccipital bone enters this recess.

The lateral face of the otic region has a complex relief (Figs 4, 5, 6, 13). Anterodorsally there is a prominent postorbital process which forms the anterior boundary of the wide spiracular groove (spig, Fig. 13). This groove passes ventromedially, crosses the otico-sphenoid fissure (fos), continues on the basisphenoid behind the basiptyergoid process and fades out on the parasphenoid at the level of the bucco-hypophysial canal (bhc, Fig. 50). There is no post-temporal fossa and this is considered primitive for actinopterygians. The post-temporal fossa is also missing in all other palaeoniscids, *Polypterus* and *Lepisosteus*, but occurs in caturids, semionotids, pycnodonts, *Amia*, pachycormids, pholidophorids and most other teleosts (Patterson 1975: 395).

The hyomandibular facet (fhm, Fig. 13) lies obliquely across the lateral commissure and is not lined by perichondral bone. Ventrally the facet extends onto the roof of the jugular canal (Figs 4, 5, 6). Behind the hyomandibular facet is an extensive raised area of bone, triangular in outline

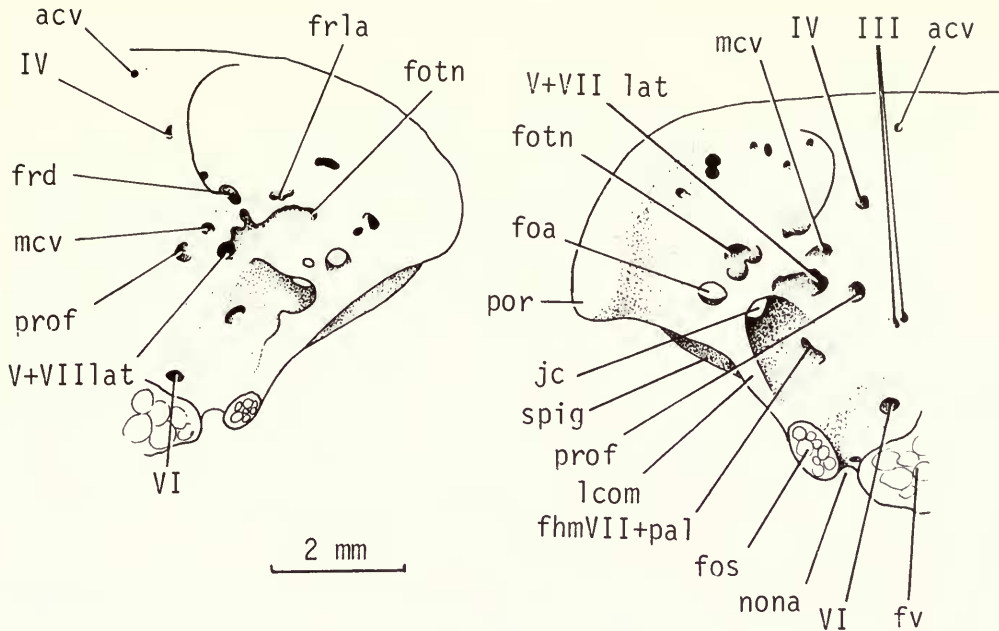


Fig. 19 *Mimia toombsi* Gardiner & Bartram. Otic and orbitotemporal regions of neurocranium in anterior view, as if cut through the middle of the orbit, from BMNH P.53234. (A), right side of the rear of the orbit; (B), left side of orbit.

with a groove or gutter dissecting it posteriorly. This area, which marks the point of origin of the dorsal hyoid constrictor muscle (oahm, oaop, Figs 4, 5, 6), stretches from the hyomandibular facet to the occipital fissure. Presumably the posterior portion of this constrictor muscle served for the adduction of the operculum (oaop, Figs 4, 5, 6) while the anteriormost region served for the adduction of the hyomandibula (oahm, Fig. 6).

Below the area of origin of the dorsal hyoid constrictor muscle a well-marked jugular groove (jg, Fig. 6) runs horizontally across the lateral face of the otic region. Behind the parampullary process (pamp, Fig. 6) the groove turns dorsolaterally in front of the vagus canal where it received the posterior cerebral vein from the upper division of that canal (gpcv, Fig. 11). The supratemporal branch of the vagus nerve (gst.X, Fig. 4) passed forward beneath the parampullary process, in the posterior portion of the jugular groove, then turned upwards and ran in a short groove through the area of origin of the dorsal hyoid constrictor muscle (gst.X, Fig. 5) and out onto the dorsal surface. Immediately beneath the posterior portion of the jugular groove there is often a further groove which soon fades out anteriorly. This groove transmitted the pharyngeal branch of the vagus nerve (gph.X, Fig. 4). The glossopharyngeal foramen (IX, Figs 4, 5, 6, 7, 13) lies either in the jugular groove or a little below it. The supratemporal branch of the glossopharyngeal nerve passed upwards from this foramen, through a distinct channel (gst.IX, Fig. 14) in the area of origin of the dorsal hyoid constrictor muscle to enter a foramen (fst.IX, Figs 4, 5, 6) immediately beneath the dermal skull roof. In some specimens this channel is confluent with that for the supratemporal branch of the vagus nerve (BMNH P.56501, P.56496, Figs 4, 6, 14), whereas in others (BMNH P.53234, Fig. 5) it is separate.

Below and in front of the glossopharyngeal foramen the wall of the saccular recess is inflated. This inflation terminates in the vestibular fontanelle (vfon, Figs 14, 15). More dorsally the ampulla of the posterior semicircular canal causes in the lateral wall a distinct swelling which is

often drawn out into a prominent, ventrally-facing, parampullary process (pamp, Fig. 6) to which the first suprapharyngobranchial was presumably ligamentously attached. In earlier reconstructions (Gardiner 1973: fig. 1) I erroneously assumed that the first suprapharyngobranchial articulated at the level of the glossopharyngeal foramen.

The lateral commissure is short and broad and composed entirely of cartilage bone. A well-marked groove (goa, Fig. 15) runs dorsolaterally from the region of the orbitonasal artery foramen up into the jugular canal. Occasionally a narrow strut of bone encloses the top of this groove (BMNH P.53234, Fig. 5). In life this groove housed the orbital artery. The orbital artery passed into the jugular canal then out into the orbit by way of one or more dorsolateral foramina (foa, Figs 16, 17, 19, 20). Immediately behind the ventral portion of this orbital artery groove there is an area devoid of perichondral bone (aip 1, Figs 13, 14, 15, 20). This area, which is directed anteroventrally, was the articulation for the first infrapharyngobranchial.

The foramen for the orbitonasal artery (fona, Figs 15, 50) is formed by two notches within the basisphenoid (nona, Figs 23, 24) and basioccipital (nona, Figs 16, 19, 20). This foramen transmitted the orbitonasal artery up into the floor of the orbit (Gardiner & Bartram 1977: 230). Lateral to this foramen the junction between the presumed prootics and basisphenoid remained cartilage-filled, as the otico-sphenoid fissure, which is found in most specimens (fos, Figs 13, 15). In one specimen (BMNH P.56483; Gardiner & Bartram 1977: fig. 3) and on one side only this fissure (Gardiner 1973: 106) has been obliterated by bone.

The jugular canal is a short longitudinal canal whose posterior opening transmitted the jugular vein, orbital artery and hyomandibular trunk of the facial nerve. The medial wall of the jugular canal (prefacial commissure and pila antotica) is ossified and there are separate facial, lateralis, trigeminal and profundus foramina. The geniculate ganglion lay in the funnel-like opening of the facial canal (fhm.VII + pal, Figs 16, 17, 19, 20, 21, 22) in the floor of the jugular canal and was clearly extracranial. From the geniculate ganglion the palatine nerve passed down into the back of the orbit and through the palatine fenestra (fpal, Fig. 20) while the hyomandibular trunk passed back laterally in the floor of the jugular canal. Dorsal to the facial canal and posterolateral to the trigeminal canal is a separate foramen (VII.lat, Figs 18, 22) which is presumed to have transmitted the lateralis branches of the facial nerve. The corresponding lateralis ganglion would have lain alongside the geniculate in the extramural chamber which opens in front of the jugular canal (V + VII.lat, Fig. 19). In some specimens distinct grooves pass from the mouth of the lateralis canal to the otic nerve foramina (fotn, Fig. 20) and to the foramen of the ramus lateralis accessorius (frla, Figs 20, 22), whereas in others (BMNH P.53234) bridges of bone convert parts of these grooves into canals (cf. Figs 17, 19). The internal opening of the lateralis canal (VII.lat, Fig. 18), which lies in the anterior opening of the utricular recess, is smaller in diameter than the internal openings of the facial and trigeminal canals. The facial canal (fhm.VII + pal, Figs 18, 26) originates outside the utricular recess and below the bridge of bone which separates the trigeminal from the lateralis root.

The external opening of the trigeminal canal (V, Fig. 22) is medial to the lateralis canal and dorsal to the facial canal. The opening is anteriorly-directed and lies in front of the jugular canal. The internal opening is twice as large as that of the facial canal and originates in front of the utricular recess. A bridge of bone internally (br, Fig. 18) separates the trigeminal root from the lateralis root. There is a separate canal for the profundus nerve (prof, Fig. 18) which originates in the anterior wall of the trigeminal canal and opens medial to the trigeminal foramen (prof, Figs 16, 19, 20, 22). Medial to the profundus foramen are two further foramina lying one above the other (III, Figs 16, 19, 20, 21); these presumably served for the two main branches of the oculomotor nerve. In two specimens only (BMNH P.56485, Fig. 22; BMNH P.53249, Fig. 25) there is a single, large oculomotor foramen as in most other actinopterygians.

The basisphenoid region (Figs 22, 23, 24) consists of a hollow vertical pillar which flares dorsally to join the orbital surface at the level of the oculomotor foramen. The basisphenoid forms the lateral and posteroventral margins of the pituitary fossa (pitf, Fig. 26) and the large hypophysial recess is open both dorsally and anteriorly. Ventrally, in the foot of the pillar, this recess leads to a narrow bucco-hypophysial canal (bhc, Fig. 26) which passes through the parasphenoid into the roof of the mouth (bhc, Fig. 50). Immediately behind the hypophysial

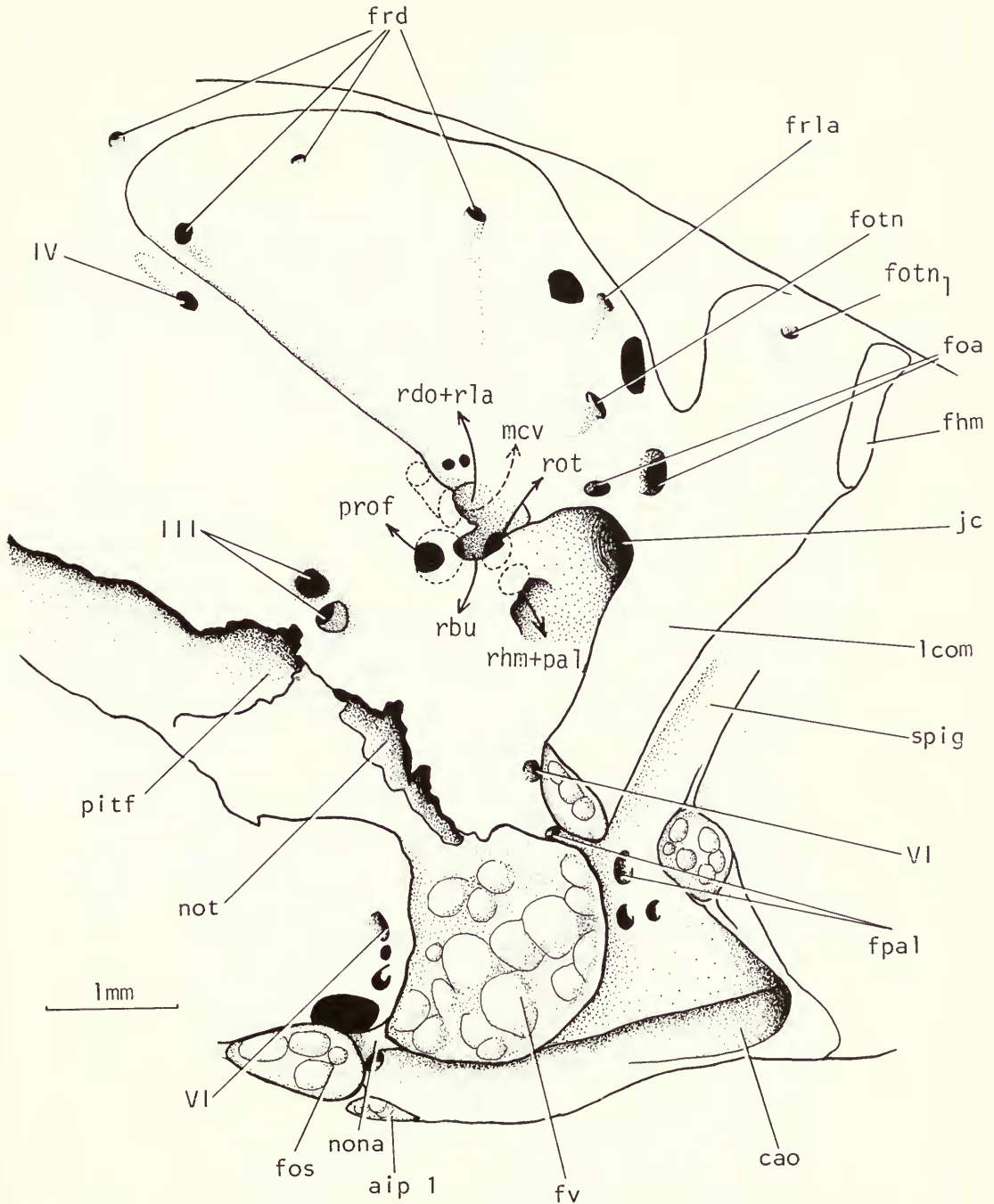


Fig. 20 *Mimia toombsi* Gardiner & Bartram. Braincase in anterodorsal view, looking up into the rear of the orbit from the left side, from BMNH P.53259. Basisphenoid missing. The arrows depict the courses of the nerves and vessels as they passed into the orbit.

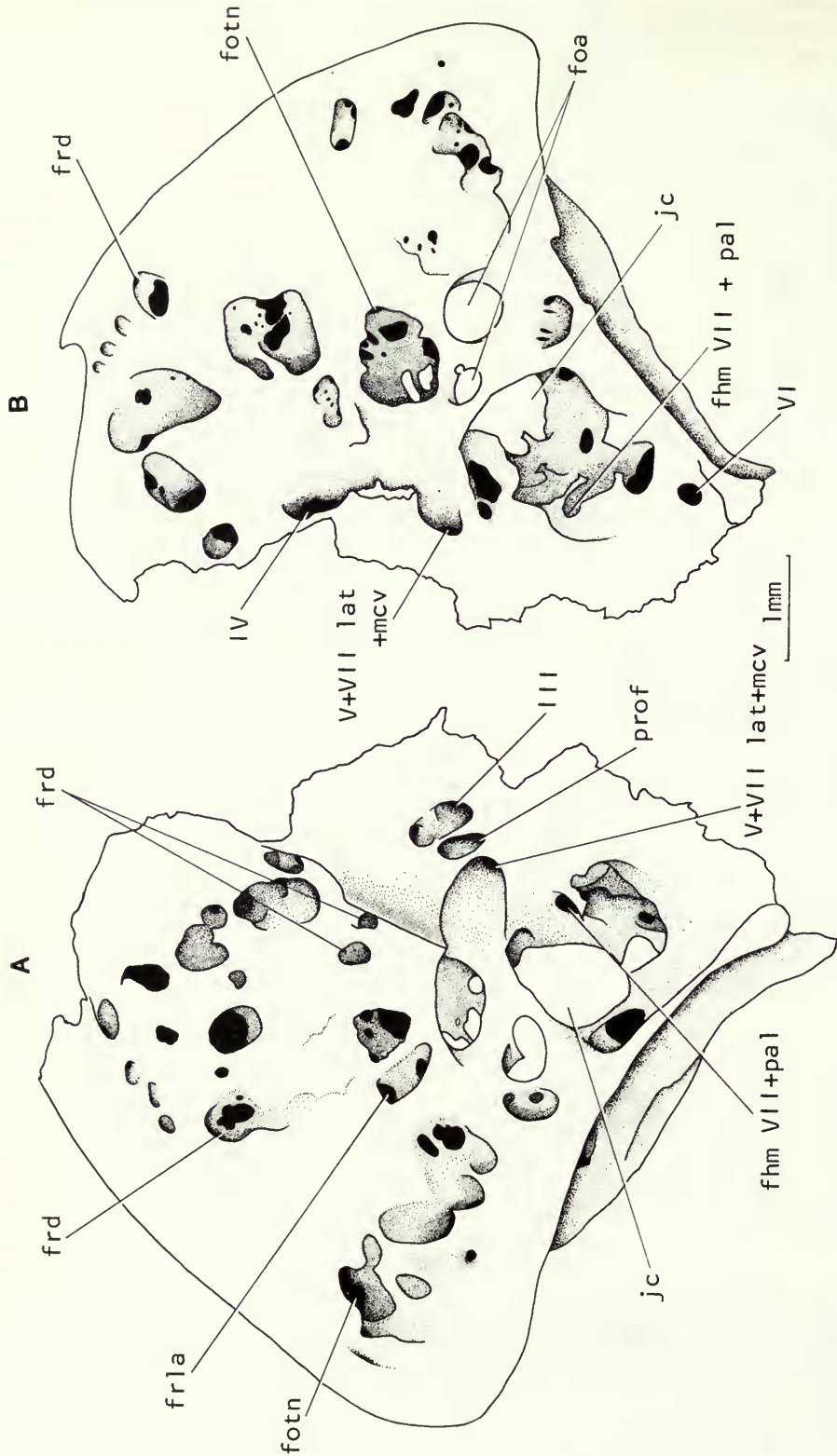


Fig. 21 *Mimia toombsi* Gardiner & Bartram. Preserved parts of the neurocranium in anterior view, from BMNH P.53245. (A), Right orbitotemporal region; (B), left orbitotemporal region.

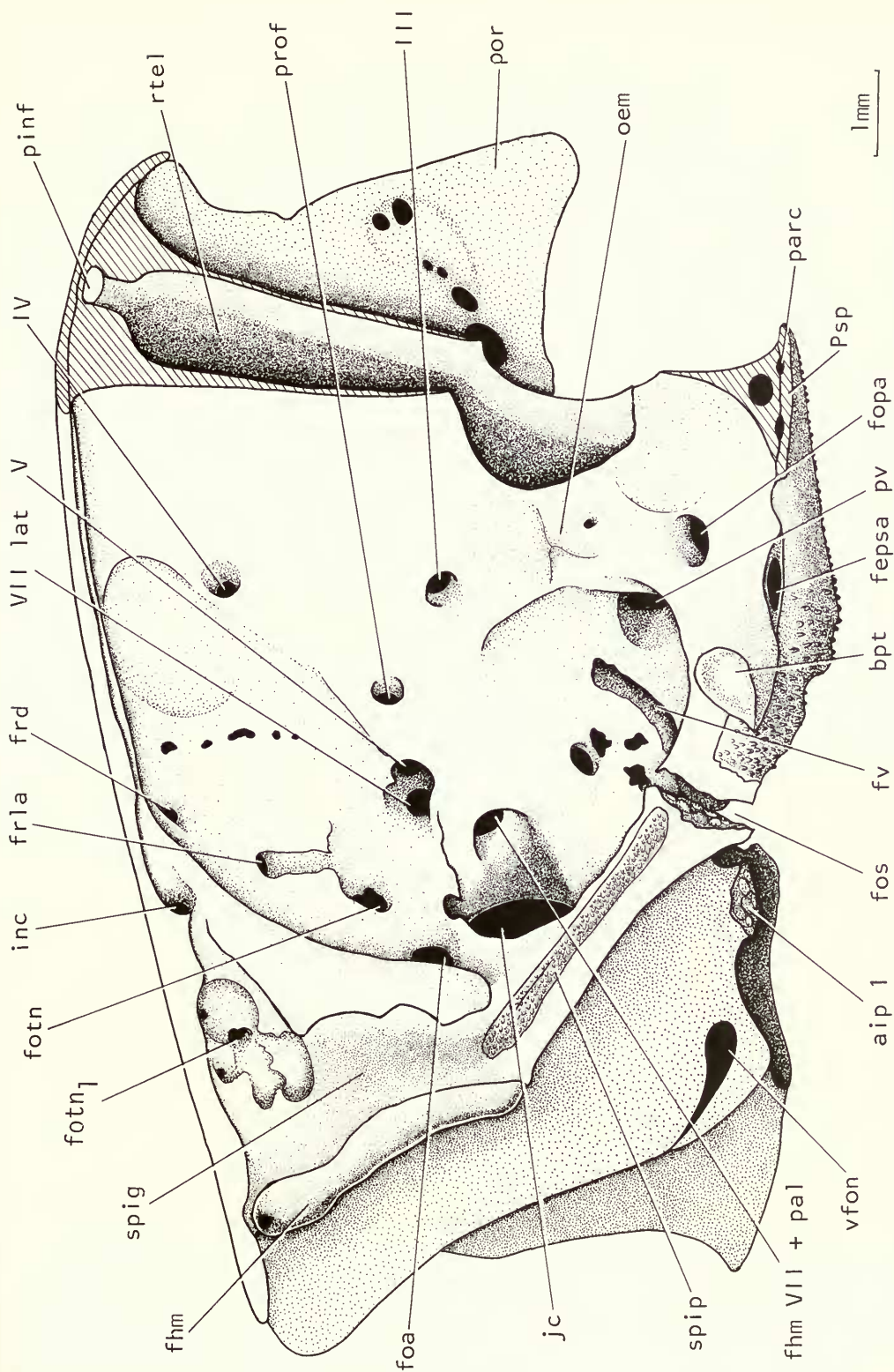


Fig. 22 *Minia toombsi* Gardiner & Bartram. Otic and orbitotemporal regions of neurocranium in oblique right anterolateral view, and as if cut through the orbit, from BMNH P.56485.

recess, in the foot of the basisphenoid pillar, ran the pituitary vein (pv, Figs 22, 23, 26). Anteriorly the space for the pituitary vein is confluent with the hypohysial recess (Fig. 23). The dorsum sellae (prob, Figs 25, 26), which forms the roof of the pituitary vein canal, is presumed to be ossified by the basisphenoid. The posterior wall of the pituitary canal is expanded into a short, stout pillar (cf. Fig. 23) which flares dorsally into the dorsum sellae. Anterodorsal to the pituitary vein canal, in the anterior surface of the dorsum sellae, is a cup-shaped depression (svr, Fig. 26). This housed the saccus vasculosus, and a median canal connecting the depression with the pituitary vein canal presumably served for the passage of the saccus vasculosus vein.

Immediately in front of the ventral otic fissure and after giving off the orbitonasal artery the internal carotid arteries entered the parabasal canal (fica, Fig. 1) in the floor of the basisphenoid. Although the parabasal canal (parc, Fig. 22) runs the whole length of the basisphenoid (between it and the parasphenoid) and opens anteriorly into the roof of the mouth, only the posterior, enlarged portion, between the ventral otic fissure and the basiptyergoid process, housed the internal carotid artery. The internal carotid arteries (Gardiner & Bartram 1977: figs 5, 6), after passing through this enlarged posterior portion of the parabasal canal, turned upwards and ran in a vertical canal in the anterior portion of the basisphenoid pillar (fica₂, Fig. 23) to enter the cranial cavity through the pituitary fossa (fica₂, Figs 24, 26). In some specimens (BMNH P.56501; Gardiner & Bartram 1977: fig. 6) the internal carotid briefly ran in a groove in the lateral wall of the basisphenoid pillar, and gave rise to an anterior branch which ran anteroventrally towards the snout in a short groove on the dorsal surface of the basisphenoid before passing down into the palatine (parabasal) canal. The palatine nerve entered the parabasal canal through an anteroventrally-directed foramen (fpal₂, Figs 23, 24), immediately in front of the ventral otic fissure, and presumably ran the entire length of the parabasal canal before emerging in the roof of the mouth at the level of the vomers. It was probably accompanied anteriorly by the palatine artery and vein.

Just in front of the basiptyergoid process a short canal runs laterally from the parabasal canal to open above the edge of the parasphenoid (fep_{sa}, Figs 13, 22, 50). This carried the efferent pseudobranchial artery which, after its anastomosis with the internal carotid (Gardiner & Bartram 1977: figs 5, 6), turned upwards and forwards through a distinct foramen (fopa, Figs 13, 22, 23, 24) into the floor of the orbit as the ophthalmic artery.

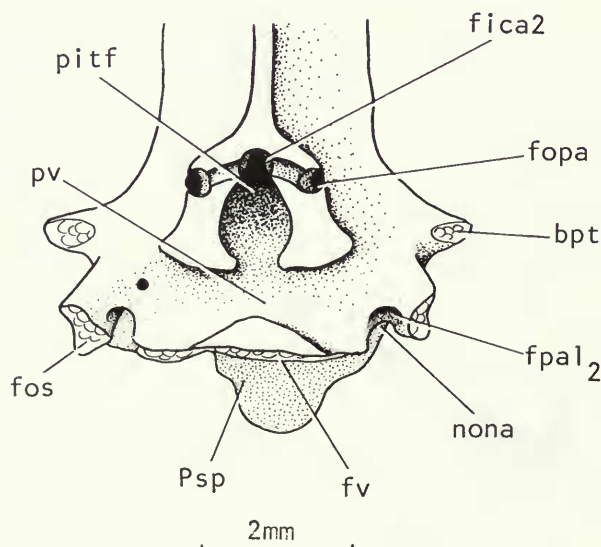


Fig. 23 *Mimia toombsi* Gardiner & Bartram. Posterior basisphenoid region of braincase cut horizontally at level of pituitary vein, in dorsal view, from BMNH P.56504.

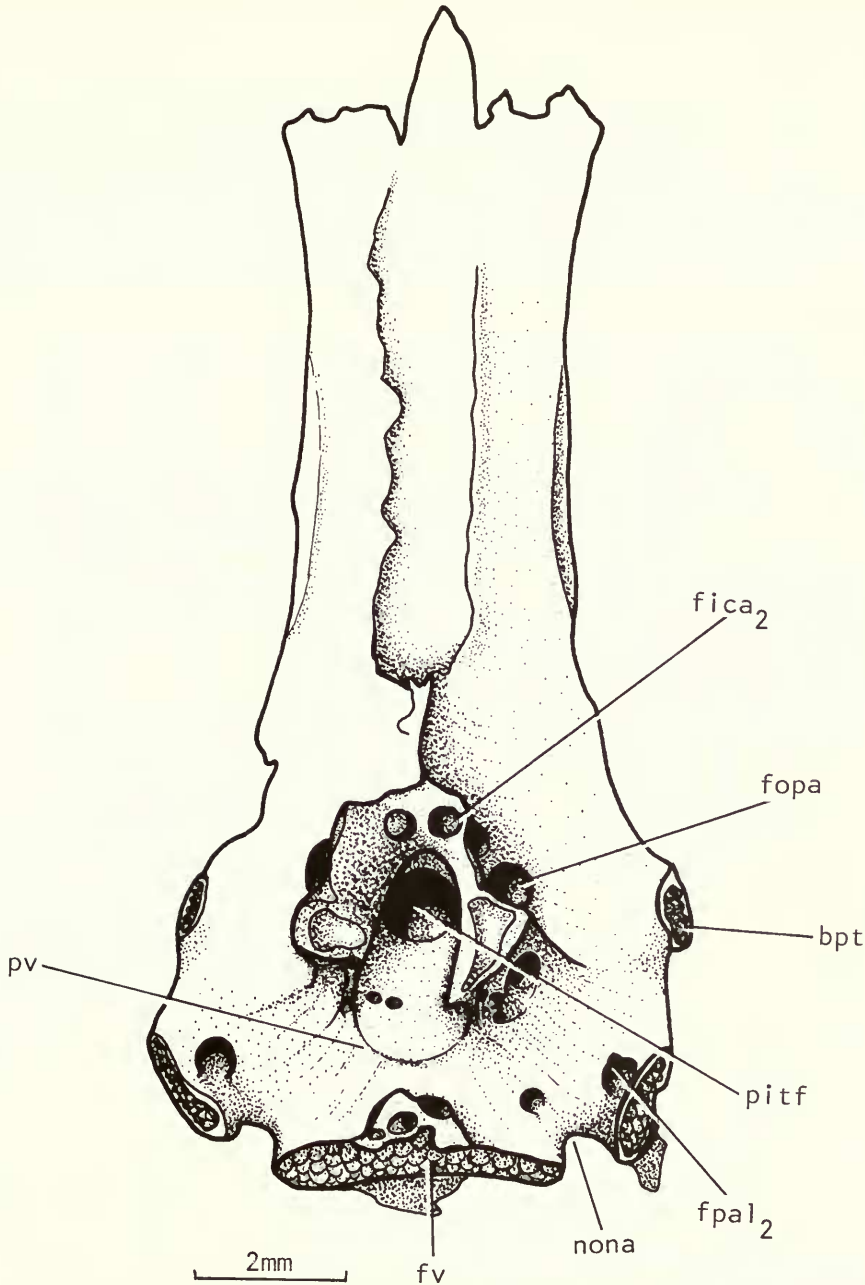


Fig. 24 *Mimia toombsi* Gardiner & Bartram. Preserved parts of basisphenoid in dorsal view, from BMNH P.53225.

On the lateral wall of the basisphenoid pillar, dorsal to the ophthalmic artery foramen, is a pronounced cup-shaped depression, divided into three components by prominent ridges (oem, Fig. 22; see also Gardiner & Bartram 1977: fig. 6). This depression must have housed at least three of the rectus muscles, but since there is not even a hint of a myodome the origin of the fourth (external) rectus muscle can only be guessed at. Perhaps it also was attached to the lateral wall of the pillar.

frontals. The two walls come very close together in the mid-line (cf. Fig. 16) and are scarcely separated by the small, median optic fenestra (II, Fig. 13).

A further foramen (mcv, Figs 18, 20) opens into the roof of the recess for the lateralis and geniculate ganglia. From this foramen a canal passes anterodorsally to open on the internal surface above the saccular recess and behind the trochlear foramen (mcv, Figs 18, 25, 26). This canal must have transmitted the middle cerebral vein. In one specimen (BMNH P.53234, Fig. 19) the canal opens above the ganglion recess. Anterior to the ramus lateralis accessorius foramen there is a series of up to four foramina (frd, Figs 20, 21, 22), which transmitted branches of the superficial ophthalmic nerves to the neuromasts of the supraorbital canal (crd, Figs 33,

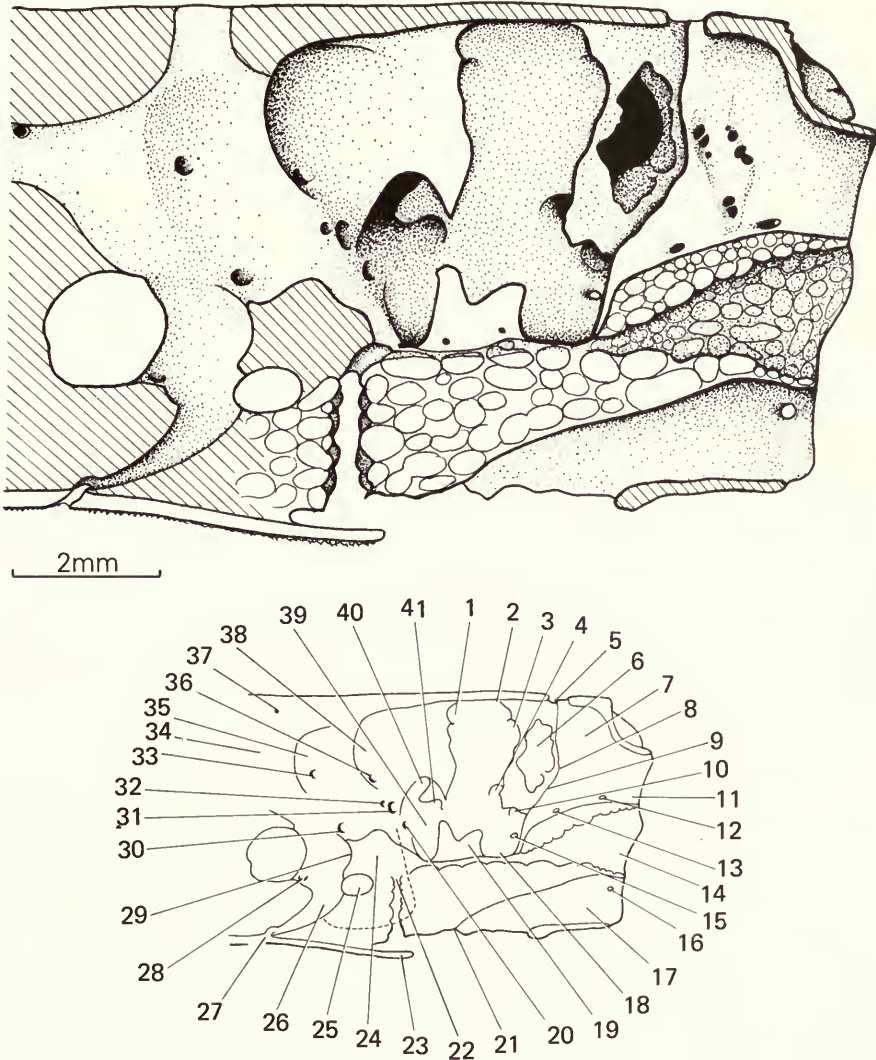


Fig. 26 *Mimia toombsi* Gardiner & Bartram. Post-ethmoid portion of neurocranium and parasphenoid in sagittal section, from the left side, based on BMNH P.53234. From Gardiner & Bartram (1977). Key (diagram below): 1, dasc; 2, dpsc; 3, ssu; 4, pesc; 5, pdf; 6, plcc; 7, rmye; 8, fote; 9, X; 10, apsc; 11, fm; 12, focn; 13, fboca; 14, not; 15, IX; 16, foca; 17, cao; 18, sac; 19, Z; 20, fhm.VII; 21, alig; 22, fv; 23, Psp; 24, prob; 25, pv; 26, pitf; 27, bhc; 28, fica₂; 29, svr; 30, III; 31, VII.lat; 32, V; 33, IV; 34, rtel; 35, ropl; 36, mcv; 37, acv; 38, rmet; 39, utr; 40, aasc; 41, aesc.

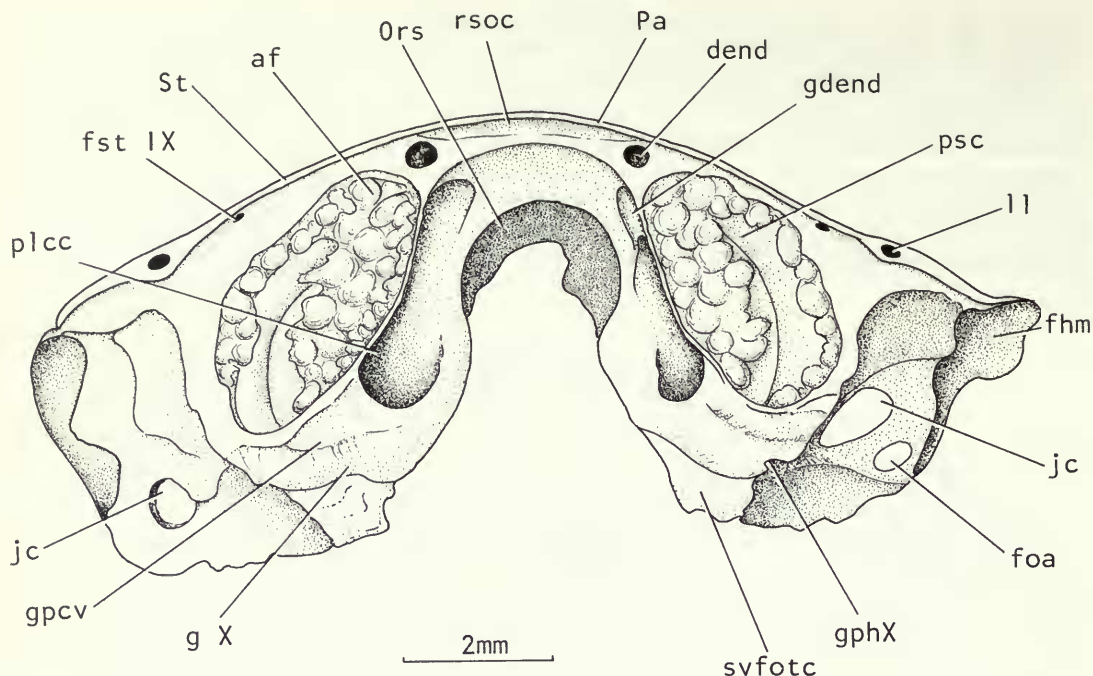


Fig. 27 *Moythomasia durgaringa* Gardiner & Bartram. Dorsal portion of otic and orbitotemporal regions of neurocranium and attached dermal bones in posterior view, from BMNH P.53227.

34). In some specimens (BMNH P.56504, Fig. 17) these branches were contained for part of their orbital course within a short canal, while in others (BMNH P.53234, P.53245, Figs 19, 21A) these branches passed up through the rim of the lateralis ganglion recess before passing out over the orbital surface and into the four dorsal foramina.

The foramen for the anterior cerebral vein (acv, Figs 13, 14, 16, 19) opens into the roof of the orbit just behind the dorsal anterior myodome (amyd, Fig. 13). It passes medially and originates in the recess housing the telencephalon (Fig. 26). Occasionally this vein was developed on the left side only (cotel, Figs 33, 34) as in the specimen of *Kansasiella* described by Poplin (1974: fig. 22) and in the *Latimeria* dissected by Robineau (1975: fig. 1A). The olfactory nerves were sheathed by perichondral bone (I, Figs 16, 33, 34, 35), but a small gap in the roof of the olfactory canal (gI, Fig. 13), where it passes beneath the floor of the dorsal anterior myodome, affords communication with the orbit.

The brain is assumed to have been closely enveloped by bone, rather more completely than in other palaeoniscids, and if so its shape and size may be accurately deduced. The relief of the brain cavity is shown in sagittal section (Fig. 26), and the dorsal extent of the cranial cavity in Figures 33, 34. The anterior dorsal fontanelle is reduced to the pineal foramen (pinf, Figs 16, 33, 34) which opens into that part of the cranial cavity which accommodated the diencephalon; the complete closure of the anterior dorsal fontanelle in adults is considered a primitive osteichthyan feature. Anterior to the diencephalon the cranial cavity is less broad where the telencephalon was housed (ctel, Figs 33, 34; rtel, Fig. 26). Anteriorly this telencephalic cavity may be overlain by inpushing of that part of the orbital wall (Pl. 1; amyd, Fig. 33) which delimits the dorsal anterior myodomies.

Posterior to the pineal foramen there is a marked increase in the breadth of the cranial cavity (copl, Fig. 33). In sagittal section this appears as a marked, rounded depression (ropl, Fig. 26) from which the trochlear nerve (IV) passed anteriorly into the orbit. This depression, which is medial to the postorbital process, contained the large optic lobe from which the optic nerves

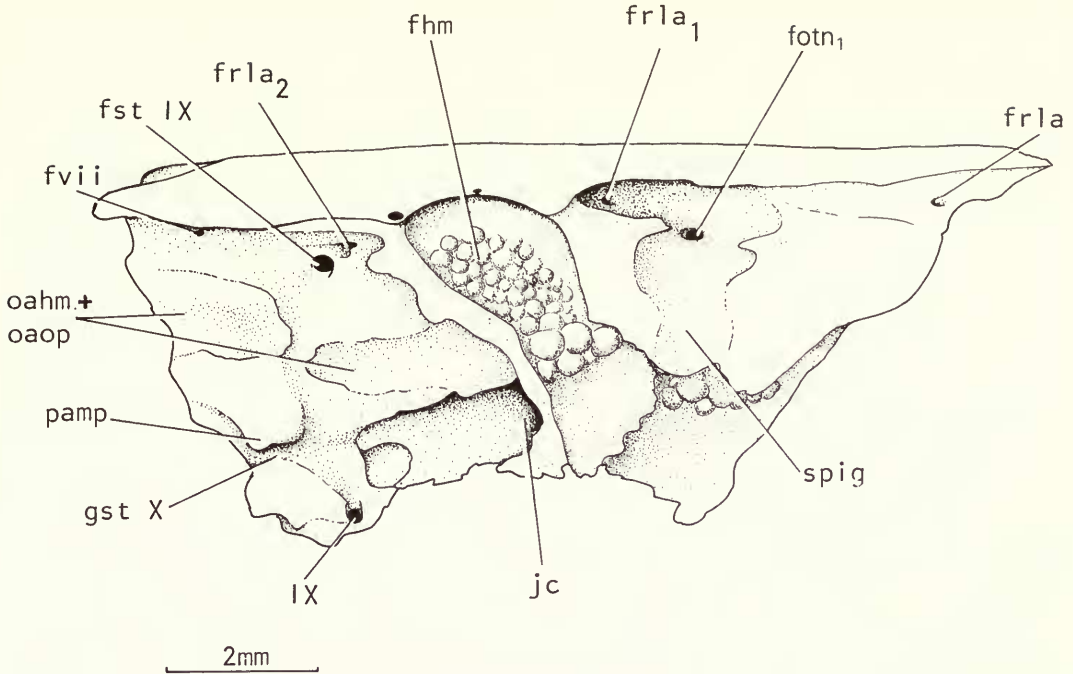


Fig. 28 *Moythomasia durgaringa* Gardiner & Bartram. Dorsal portion of otic and orbitotemporal regions of neurocranium and attached dermal bones in right lateral view, from BMNH P.53227.

passed out anteroventrally through the optic fenestra (II). The cranial cavity beneath the optic lobes decreases rapidly in breadth and is floored by the 'prootic' bridge (dorsum sellae, prob, Fig. 26). The walls in this region are perforated by the oculomotor foramen (III) and the floor in front of the 'prootic' bridge by the pituitary fossa (pitf, Fig. 26). A further strong depression (rmet, Fig. 26) behind the optic lobes and above the anterior ampullary chamber (aasc, Fig. 26) and utricular recess (utr, Fig. 26) accommodated the cerebellum. The middle cerebral vein (mcv) left the anteroventral corner of this depression on its way to the orbit. Below the cerebellum the walls of the cranial cavity decrease in breadth much as beneath the optic lobes and are perforated by the foramen for the trigeminal plus profundus nerves (V, Figs 18, 26) and the foramen for the hyomandibular and palatine trunk of the facial nerve (fhm.VII + pal, Fig. 18). The lateralis branch of the facial nerve (VII.lat, Figs 18, 26), however, passed out through the front of the recess for the utriculus (utr, Figs 18, 26).

There is a wide communication between the cranial and labyrinth cavities, as in other palaeoniscids, *Polypterus*, *Acipenser*, *Lepisosteus* and *Amia*. Nevertheless the labyrinth cavity is mostly enclosed within the bony walls of the otic region. The saccular recess is extensive and in the form of an almost square pocket similar in size and shape to that of *Pteronisculus* (Nielsen 1942: fig. 14) but deeper than in *Pholidophorus* (Patterson 1975: fig. 66). Although this pocket is in wide communication with the cranial cavity above, the zygial plates (Z, Fig. 26) form an inner, dorsal wall to the pocket separating it (and the contained sacculus) from the floor of the brain.

From the serial sections it can be seen that a single otolith is present in each saccular recess. It appears to be longer than deep and relatively compact. The glossopharyngeal nerve passed through the dorsoposterior part of the saccular recess. Immediately above the glossopharyngeal foramen (IX, Fig. 26) and below the opening of the lateral cranial canal there is a deep recess which housed the ampulla of the posterior semicircular canal (apsc, Figs 25, 26). The sinus superior lay in front of and medial to the opening of the lateral cranial canal in a distinct concavity (ssu, Fig. 26) in the cranial wall. Ventrally, in the region of the recess for the posterior ampullary

chamber, a flange of bone forms a partial posterior boundary to the sinus superior recess. A similar flange of bone is found in *Pholidophorus* (Patterson 1975: fig. 65). A dorsal opening at the front of the ampullary recess marks the exit of the external semicircular canal. Thus this canal must have passed laterally through the anterior part of the ampullary recess as in *Kansasiella* (Poplin 1974: fig. 20), *Perleidus*, *Ospia*, *Caturus* and *Pholidophorus*, whereas in other palaeoniscids such as *Pteronisculus*, *Kentuckia* and *Boreosomus* the openings of the posterior ampullary recess and the external canal are separated by a small pillar of bone. At the top of the groove for the sinus superior lie the dorsal openings of the anterior (dasc, Fig. 26) and posterior (dpasc) semicircular canals. The anterior semicircular canal is considerably longer than the other two canals and anteriorly enters its ampulla (aasc, Figs 18, 26) in the anterodorsal portion of the utricular recess. The external ampullary chamber (aesc, Figs 18, 26) lay in a posterior diverticulum of the utricular recess behind and below a well-marked projection on the posterior margin of the entrance to this recess. A similar projection has been described in *Pholidophorus* (Patterson 1975: fig. 65) and in the dipnoan *Griphognathus* (Miles 1977: fig. 10).

Between the posterior semicircular canal and the recess for the sinus superior is an intramural lateral cranial canal (lcc, Fig. 12). Posteriorly this canal opens into the cranial cavity (plcc, Figs 12, 25, 26) above the posterior ampullary recess and in front of the occipital fissure. This lateral cranial canal (Jarvik 1980) is reduced to a small pocket in many specimens, where it is similar in extent to that described in *Kentuckia* (Rayner 1951: fig. 9, X) and *Kansasiella* (Poplin 1974: fig. 20, elmy). In other less well ossified specimens the canal is more extensive (Fig. 12) and may even communicate with the cranial cavity anteriorly (in front of the sinus superior) by several small foramina. In other individuals the roof of the canal is fenestrated and widely open dorsally. A lateral cranial canal is present in most palaeoniscids, Recent chondrosteans, *Perleidus*, *Lepisosteus*, most halecomorphs, pholidophorids and leptolepids.

The sclerotic ring is well preserved and usually consists of either a complete ring or two segments, each comprising three separate layers of bone. The outer layer is dermal and ornamented with ridges of ganoine which run more or less concentrically round the ring (BMNH P.56483), whereas the underlying layers (inner and outer) are made up of very thin perichondral bone (BMNH P.56496). Where there are two segments the two halves are disposed dorsally and ventrally, not fore and aft of the eyeball as in teleosts and fossil halecomorphs. In one specimen of *Mimia*, however, there are three separate segments and in another, presumably a juvenile (BMNH P.53258), there are four separate plates. The innermost part of the sclerotic is ossified as a thin, perichondral, basal sclerotic bone around the entry of the optic nerve and vessels (BMNH P.53228). This basal sclerotic bone is cup-shaped and like the outer perichondral layer which underlies the dermal ring, has a corresponding inner layer of perichondral bone. Thus, bone is developed on both surfaces of the sclerotic cartilage as in other primitive actinopterygians (Patterson 1975: 415), placoderms and agnathans (see p. 253).

Moythomasia durgaringa

The posterior face of the otic region is only partially lined with perichondral bone. A large ovoid area (af, Fig. 27), stretching from just above the vagus canal almost to the opening of the endolymphatic duct, has no perichondral lining and must have been cartilage-filled during life. A similar loss of the perichondral lining is presumed to have occurred early in the phylogeny of dipnoans and osteolepiforms (Gardiner 1973: 111). A notch (gph.X, Fig. 27) in the groove for the vagus nerve served for the passage of the pharyngeal branch of that nerve as in some specimens of *Mimia*, but the foramen for the endolymphatic organ (dend) is considerably larger than the corresponding foramen in *Mimia*. The lateral face of the otic region (Fig. 28) only differs from that of *Mimia* in the more ventral position of the raised areas for the origin of the dorsal hyoid constrictor muscle (oahm + oaop).

The jugular canal is a trifle longer than in *Mimia* and the orbital artery entered posteriorly by a separate vertical canal (goa, Fig. 7). In one specimen (BMNH P.53227, Fig. 31), in which the orbital region is broken open, the individual canals for the various nerves opening into the jugular canal can be recognized as distinct tubes of perichondral bone.

The facial canal (VII, Fig. 31), which transmitted the palatine and hyomandibular trunk of the

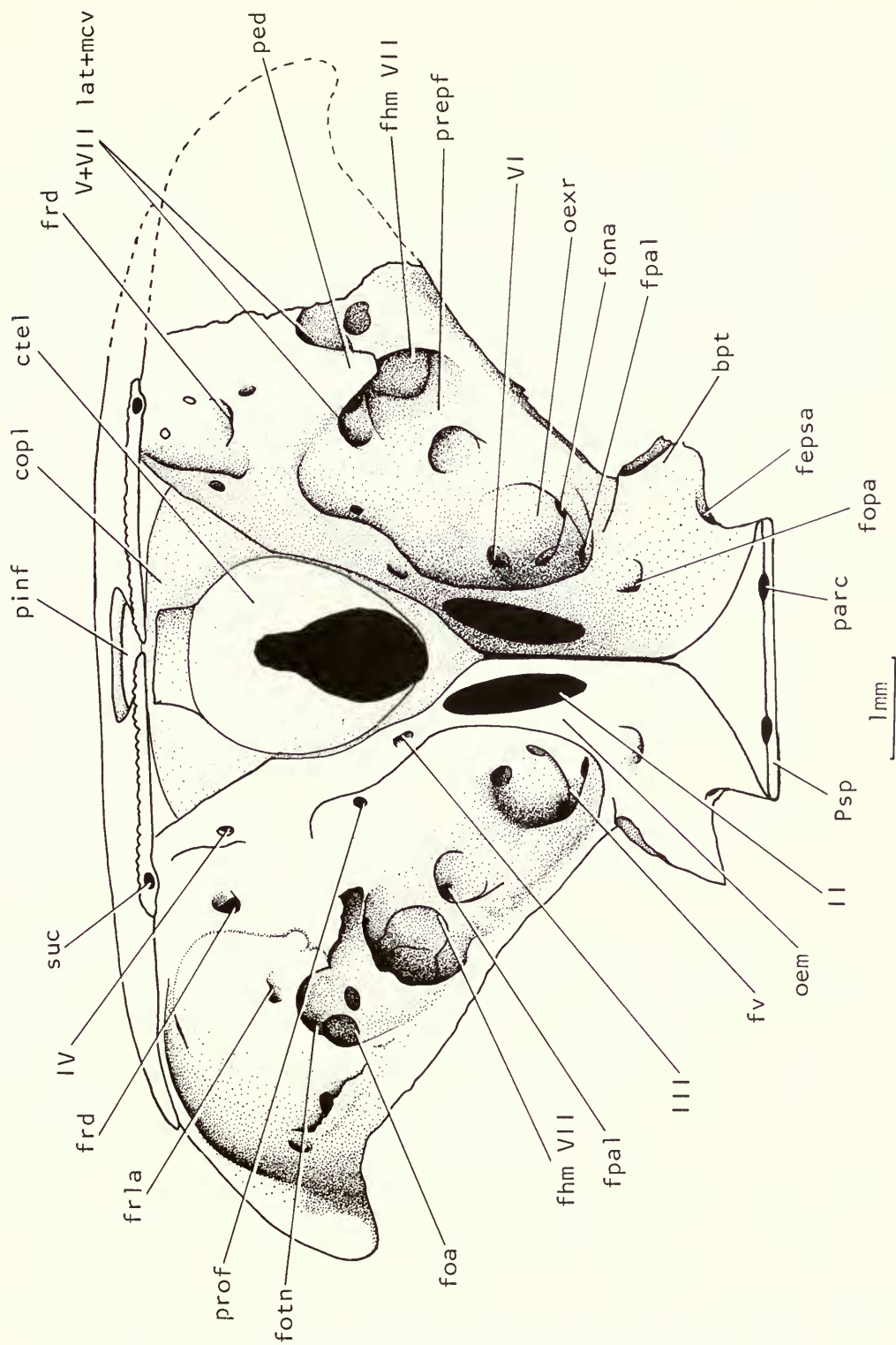


Fig. 29 *Myothomasia durgaringa* Gardiner & Bartram. Preserved parts of neurocranium and attached roofing bones in anterior view, from BMNH P.53255.

facial nerve, opens into the ventromedial corner of the orbital opening of the jugular canal. This external opening is confluent with a palatine fenestra (fpal, Fig. 29) in which the geniculate ganglion must have lain. Thus *Moythomasia* is unique amongst palaeoniscids in possessing a prepalatine (or prefacial) floor (prepf, Fig. 29) to the jugular canal.

Lying immediately above the facial canal the lateralis canal (VII.lat, Fig. 31) opens together with the trigeminal canal (V, Fig. 31) into a large pocket in the mouth of the jugular canal, dorsal to the palatine fenestra. This pocket must have housed both the lateralis and gasserian ganglia. Two grooves in the medial wall of this pocket run upwards from the mouth of the lateralis canal. One of the grooves passes up towards the foramen for the otic nerve and must have transmitted the otic branch (rot, Fig. 31), while the more medial groove served for the dorsal branch of the superficial ophthalmic nerves and the recurrent branch of the facial nerve (rdo + rla). From this medial groove the ophthalmic and recurrent branches entered a short canal to re-emerge in the back of the orbit (frd, Fig. 29) before finally entering separate foramina in the orbital roof (frla, frd, Fig. 30). The trigeminal canal runs dorsal to the lateralis canal with the canal for the profundus (prof) running anterior to both. The profundus canal has a separate internal opening, whereas externally it opens in front of the pocket for the gasserian and lateralis ganglia (prof, Figs 29, 30). A pedicel of bone (ped, Figs 29, 30) often covers this pocket and is homologous with the pterosphenoid pedicel in *Amia* and *Pholidophorus*. In some specimens (BMNH P.56480, Fig. 30) it is complete and spans the mouth of the jugular canal. A further foramen beneath the posterior margin of the pterosphenoid pedicel is presumed to have transmitted the middle cerebral vein (mcv, Fig. 31).

The internal carotid artery, after passing through the enlarged posterior portion of the parabasal canal, turned upwards to emerge in the floor of the orbit in the foot of the basisphenoid pillar (fopa, Figs 7, 32), from whence the ophthalmic artery ran forwards along the

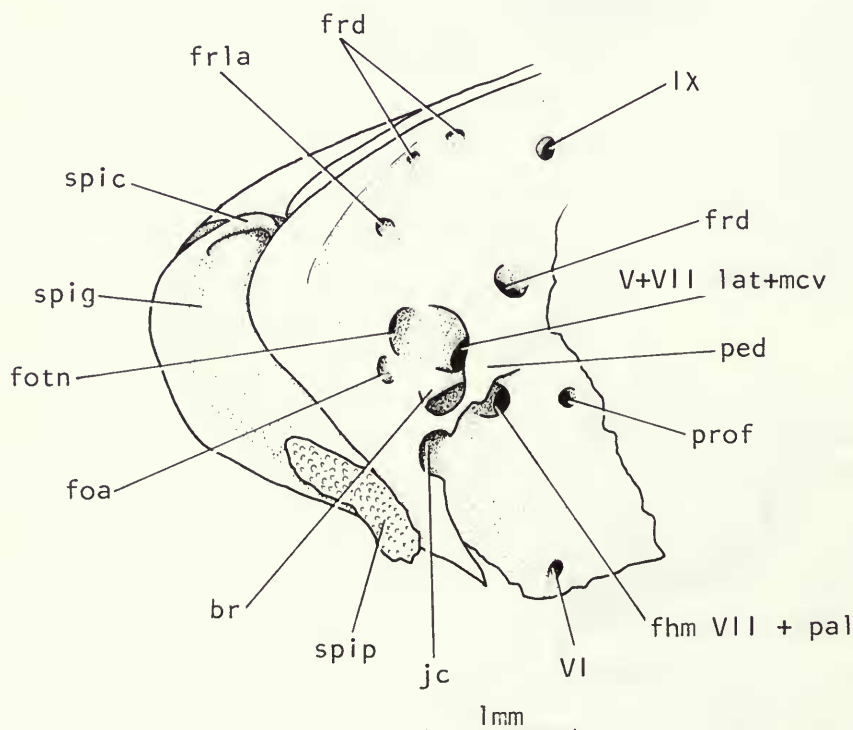
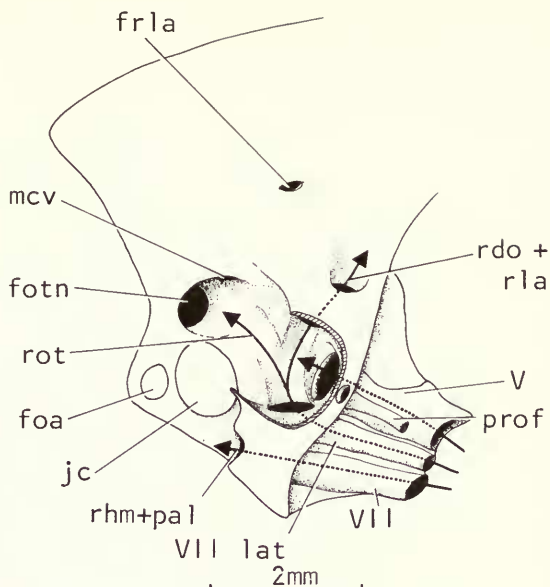


Fig. 30 *Moythomasia durgaringa* Gardiner & Bartram. Preserved part of the rear of the right orbit in oblique anterolateral view, from BMNH P.56480.

Fig. 31 *Moythomasia durgaringa* Gardiner & Bartram. Sketch of the rear of the right orbit in anterior view, from BMNH P.53227. Mouth of the trigeminofacial chamber is drawn as if cut away, and the cut surface cross-hatched. The passage of individual nerves is represented by arrows.



floor of the orbit while the internal carotid ran upwards in a groove in the anterolateral wall of the basisphenoid pillar to enter the cranial cavity through the pituitary fossa.

Muscle scars, in the form of two distinct cups, one above the other, are present on the basisphenoid bolster dorsal to the foramen for the internal carotid artery, in an identical position to those in *Mimia*. Whether or not the external rectus muscle originated here or in the back of the orbit ventrolateral to the abducens foramen (oexr, Fig. 29) could not be determined with certainty. However, the otico-sphenoid fissure is closed by bone anteriorly and laterally, where the ascending process of the parasphenoid bridges it, but posteriorly it is open for a short distance (fos, Fig. 7).

The sclerotic ring consists of two segments of dermal bone as in some specimens of *Mimia*, but no evidence of perichondral ossifications could be found. In the closely allied *Moythomasia nitida* four dermal plates have been described (Jessen 1968: fig. 12).

Otic and orbitotemporal region: discussion

1. *Parampullary process*. This is a prominent feature of the opisthotic in *Mimia* and *Moythomasia*, and is also prominent in *Kentuckia* (Rayner 1951: fig. 7), *Birgeria* (Nielsen 1949: fig. 60), '*Ambipoda*' (Beltan 1968: pl. 6) and *Australosomus* (Nielsen 1949: fig. 7). In *Polypterus* the opisthotic ossifies late in ontogeny from a centre over the base of the posterior semicircular canal and in the adult it is a large ossification with extensive membrane bone components. It has a strongly-developed ridge extending dorsoposteriorly along its length. Under this ridge the hyomandibular and opercular adductor muscles take origin and the branchial levator muscles originate more posteriorly. The posterior portion of this opisthotic ridge in *Polypterus* is taken to be the homologue of the parampullary process in palaeoniscids, and the parampullary process is taken to have developed primitively in relation to the branchial levator muscles. No parampullary process as such is present on the opisthotic of *Perleidus* or parasemionotids, though it seems likely that the branchial levator muscles must have been attached to this bone, since the intercalar is still small and has not grown over the cranial fissure. In more advanced actinopterygians the parampullary process is often difficult to recognize because that region of the opisthotic on which the branchial levator muscles originate has been captured by anteroventrally-directed membrane outgrowths from the intercalar. Thus in *Amia* the branchial levator muscles originate entirely on the membranous intercalar. Presumably most of these

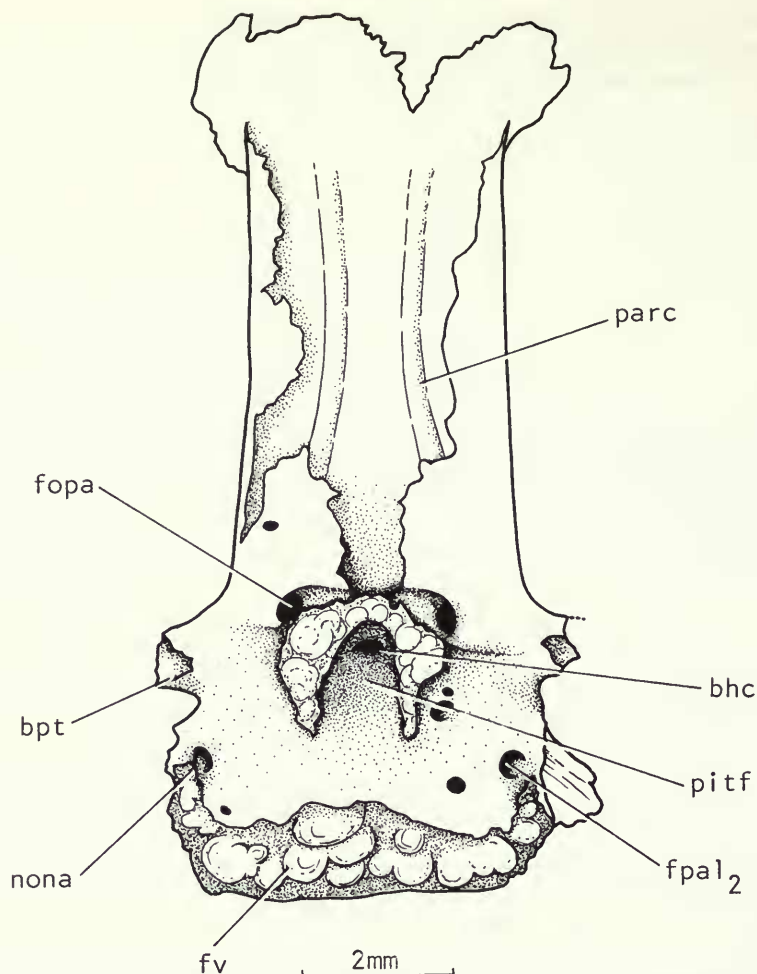


Fig. 32 *Moythomasia durgaringa* Gardiner & Bartram. Preserved parts of basisphenoid in dorsal view, from BMNH P.53219.

muscles originated on the intercalar in caturids also, but in '*Aspidorhynchus*' (Patterson 1975: fig. 99, prlm), *Macrepisteus* (Schaeffer 1971: fig. 5) and *Heterolepidotus* (Gardiner 1960: fig. 29) a knob on the surface of the prootic must have served for the origin of at least the anteriormost branchial levators.

In Devonian dipnoans the adotic process, a knob which arises from the ventral edge of the jugular groove behind the glossopharyngeal foramen, homologous with the adotic eminence of Devonian actinistians (*Nesides* Bjerring 1977: fig. 23A) and the 'process for the attachment of adductor muscles of hyomandibula' of *Eusthenopteron* (Bjerring 1971: fig. 8), is said by Miles (1977: 79) to be a similar outgrowth to the caturid prootic knob. But since the adotic process lies partly below the jugular canal it seems more likely that it received either the ventral portion of the first branchial levator muscle, which in *Polypterus* is attached to the parasphenoid, or the ceratobranchial ligament (cf. *Polypterus*, Allis 1922: 234). In pholidophorids, where the intercalar has extensive membrane bone outgrowths covering the adjacent otic bones, the parampullary process of the opisthotic can still be recognized (Patterson 1975: fig. 61, ampp). In pholidophorids and Upper Jurassic leptolepids struts of bone from the prootic and intercalar unite to form a bridge over the subtemporal fossa. *Elops* and *Osteoglossum* have a similar bridge, and here the branchial levator muscles originate, as well as the ligamentous attachment

of the first suprapharyngobranchial. There is a distinct parampullary process in actinistians which is borne on the opisthotic in *Macropoma*, *Laugia* and *Wimania*. In the Recent *Latimeria* a cartilaginous process in an homologous position is the origin of both the branchial levator muscles and the ligament of the suprapharyngobranchial. A parampullary process may also be recognized in rhipidistians such as *Ectosteorhachis* (Romer 1937: figs 2, 4, 5, popcp ?) where its relationships to the foramina for the glossopharyngeal and vagus nerves (particularly the supratemporal branches) are exactly as in *Mimia* and *Moythomasia*. A similar process in *Eusthenopteron* (Jarvik 1954: fig. 1, prpo) also served as a point of articulation for the first suprapharyngobranchial. In the Devonian dipnoan *Griphognathus* (Miles 1977: 79) a small ventral outgrowth from the upper margin of the jugular groove, between the foramina for the vagus and glossopharyngeal nerves, may also have given origin to branchial levator muscles. No such process has been described in acanthodians, placoderms or chondrichthyans. The presence of a parampullary process on the opisthotic is presumed to be a primitive osteichthyan character.

2. *Articulation of first suprapharyngobranchial.* In the Gogo palaeoniscids there is no obvious facet for the articulation of the spatulate first suprapharyngobranchial. It rested against or articulated with the opisthotic region of the braincase in front of the parampullary process and below the jugular canal (Fig. 119). In *Polypterus*, while there is no suprapharyngobranchial as such, the first epibranchial articulates with the opisthotic below the jugular canal and in front of the glossopharyngeal foramen (Devillers 1958: 665). In sturgeons the first suprapharyngobranchial articulates with the opisthotic (when present) below the jugular canal, but the second suprapharyngobranchial articulates with the braincase above the jugular canal (Bertmar 1959: 305, 329). The first suprapharyngobranchial also articulates with the otic region in *Polyodon* (Bridge 1878). In *Amia*, as in *Polypterus*, there is no suprapharyngobranchial. In *Lepisosteus* the cartilaginous first suprapharyngobranchial does not articulate with the braincase: it lies behind the glossopharyngeal nerve. In teleosts which have retained an ossified first suprapharyngobranchial such as *Elops*, and other members of the families Elopidae and Alepocephalidae, this element inserts by a ligament together with the branchial levator muscles on the intercalar strut. The first pharyngobranchial in *Latimeria* is also in ligamentous attachment to the parampullary process (Millot & Anthony 1958) and in *Eusthenopteron* (Jarvik 1954: fig. 23) the pharyngobranchial is said to articulate directly with that process.

Elsewhere in actinopterygians the pattern is variable. In *Birgeria* (Nielsen 1949: fig. 60) the suprapharyngobranchial articulated with a distinct facet, lacking perichondral lining, on the parampullary process of the opisthotic, as in *Eusthenopteron*. On the other hand in *Pteronisculus* (Nielsen 1942: 196) the first suprapharyngobranchial articulated with a large facet lacking perichondral lining on the posteroventral portion of the opisthotic below the glossopharyngeal foramen. This articulation is below the jugular groove and is in a similar position in *Mimia*, *Moythomasia* and *Acipenser*. A smaller, paired articular surface, lying rather more anteriorly but still below the jugular canal, served for the articulation of the first suprapharyngobranchial in *Kansasiella* (Poplin 1974: fig. 13). In the pholidopleurid *Australosomus* (Nielsen 1949: fig. 37) the articular facet is in an identical position to that in *Pteronisculus*. In caturids (*Caturus* Gardiner 1960: fig. 36; '*Aspidorhynchus*' Patterson 1975: fig. 99, asup.1; *Heterolepidotus* Patterson 1975: fig. 102, asup.1; *Osteorachis* Patterson 1975: 397) the articular area is equally distinct, and as in *Pteronisculus*, *Kansasiella* and *Australosomus* lies just below the glossopharyngeal foramen, in a notch in the margin of the intercalar. Elsewhere within amioids an articular facet is not recognizable nor is one to be seen in semionotids, pachycormids or leptolepids. The only other recorded occurrence of a distinct facet for the articulation of the first suprapharyngobranchial is in pholidophorids, where it is said to lie below the jugular groove on the prootic, midway between the glossopharyngeal and facial foramina (Patterson 1975: 397). This position is considerably more anterior and more ventral than in any other actinopterygian, rhipidistian or actinistian. It seems likely that this facet on the prootic was not for the first suprapharyngobranchial (which was probably in ligamentous contact with the intercalar strut as in *Elops*) but for the second infrapharyngobranchial. The second infrapharyngobranchial in *Elops* lies in close proximity to the posterior portion of the prootic,

with its head in a similar position to the facet described by Patterson (1975: fig. 56, asup.1) in *Pholidophorus*. The second infrapharyngobranchial also articulates with the braincase in *Acipenser* and *Polyodon* (in front of the vagus foramen) and in *Eusthenopteron* where it articulates with the basioccipital region (as does the first infrapharyngobranchial). The condition in *Eusthenopteron* is similar to *Australosomus* (Nielsen 1949: 122) except that in the latter the second infrapharyngobranchial merely lies adjacent to the underside of the basioccipital.

There are no known pharyngobranchials in dipnoans (Miles 1977: 287) but cartilaginous nodules are said to underlie the medial ends of the epibranchials in *Neoceratodus* (Nelson 1968: fig. 5D). Since no suprapharyngobranchials are known in placoderms, chondrichthyans or acanthodians they are presumed to be a derived feature of osteichthyans (Rosen *et al.* 1981; see also under branchial arches, p. 362).

3. *Articulation of first infrapharyngobranchial.* In *Mimia* and *Moythomasia* the articulation of the first infrapharyngobranchial is represented by an area devoid of perichondral lining at the posteroventral corner of the prootic, posterior to the ventral otic fissure and immediately behind the groove for the orbital artery. Elsewhere in osteichthyans the first infrapharyngobranchial (= pharyngobranchial) articulates with the braincase posterior to the ventral otic fissure in the actinopterygian *Cosmopterygius* (Schaeffer 1971: fig. 8), and in the rhipidistians *Eusthenopteron* (Jarvik 1954: fig. 1) and *Ectosteorhachis* (Romer 1937: fig. 2). In most actinopterygians the articulation lies anterior to the fissure owing to the presumed posterior migration of the ventral otic fissure (Gardiner 1970; Gardiner & Bartram 1977). Possible exceptions to this are *Polypterus*, *Polyodon* and *Acipenser*, in which the limits of the fissure are not precisely determinable, and *Australosomus* (Nielsen 1949: 122) in which the articulation straddles the ventral otic fissure. As a result of the rearward growth of the parasphenoid in *Polypterus*, later palaeoniscids and higher actinopterygians (Gardiner 1973: 115) the first infrapharyngobranchial has often become secondarily associated with it. Thus the first infrapharyngobranchial articulates with the parasphenoid in *Pteronisculus* (Nielsen 1942: fig. 45), *Polypterus*, *Acipenser*, *Amia*, *Lepisosteus*, Upper Jurassic leptolepids (Patterson 1975: 398) and many other teleosts, whereas in *Polyodon* it articulates in the notch between the ascending and posterior processes of the parasphenoid. In pholidophorids (Patterson 1975: 398), parasemionotids, most caturids (*Caturus*, Patterson 1975: 398; *Heterolepidotus*, Patterson 1975: fig. 102; '*Aspidorhynchus*', Patterson 1975: fig. 99), pachycormids (*Pachycormus*, Patterson 1975: fig. 106) and semionotids (*Dapedium*, Patterson 1975: fig. 112; *Lepidotes*, Patterson 1975: fig. 108) the situation is as in *Polyodon* except that there is a well-marked facet on the prootic and a notch in the overlying parasphenoid. In all these actinopterygians the articulation remains (as far as can be deduced in the fossil forms) approximately on the level at which the lateral aortae give rise to the orbital arteries. Primitively then in osteichthyans the first infrapharyngobranchial articulated with the prootic behind the ventral otic fissure and orbital artery.

The pharyngobranchials of acanthodians are homologous with those of selachians and with osteichthyan supra+ infrapharyngobranchial (see p. 362). The pharyngobranchials of selachians and acanthodians project posteromedially (Nelson 1968; Miles 1973a: 96; Jarvik 1977: fig. 8) and this is primitive for gnathostomes. Pharyngobranchials in chondrichthyans and placoderms are usually located posterior to the neurocranium, but in *Heterodontus* and several other sharks as well as holocephalans the first pharyngobranchial lies close to the underside of the occiput though never articulating with it. This latter condition is considered to be derived, as suggested by Miles (1971a).

According to Miles (1973a: 88) the second pharyngobranchial in *Acanthodes* articulated with the ventral occipital ossification by a facet just behind a groove for an efferent branchial artery. This would be impossible if the pharyngobranchial were backwardly projecting; I suggest the facet may have served for the articulation of the first epibranchial.

The change in branchial arch suspension in osteichthyans, with the development of the forwardly-directed first infrapharyngobranchial (articulating with the braincase) and the development of the suspensory first suprapharyngobranchial, is presumed to be related to the

increasing importance of the levator arcus palatini muscles and to the hyoid bar pump in expanding the orobranchial chamber.

4. *Lateral commissure and trigeminofacialis chamber.* The lateral commissure is penetrated by the jugular canal and forms the side-wall to the trigeminofacialis chamber in osteichthyans. It was first described in actinopterygians (*Amia*, *Lepisosteus*, *Salmo*), where it is formed (de Beer 1926: 332; 1937: 391) by the junction of the prootic process (developed from the otic capsule) with the basitrabecular and postpalatine processes (developed from the edge of the basal plate).

There has been much discussion as to whether the lateral commissure has a neurocranial or visceral origin. In actinopterygians there is little doubt that the commissure is entirely neurocranial in origin according to the work of Swinnerton (1902) on *Gasterosteus*, de Beer (1926, 1937) on *Amia* and *Salmo*, Hammarberg (1937) on *Lepisosteus*, Hubendick (1943) on *Leuciscus*, Daget & d'Aubenton (1957) on *Heterotis* and Bertmar (1959) on *Hepsetus*. Only Holmgren (1943: 33, 37, 42) suggested that the lateral commissure in actinopterygians is a visceral structure, because in *Acipenser*, *Amia* and *Lepisosteus* he found a membranous basal connection between the palatoquadrate and trabecular region, which he homologized with the spiracular cartilages in sharks. Since there is no suggestion of a transfer of cartilage from the palatoquadrate (or any other visceral source) to the neurocranium Holmgren's assumptions seem ill-founded. Bertmar (1959: 339) reinvestigated Holmgren's (1943) material and concluded that the lateral commissure in *Acipenser*, *Amia* and *Lepisosteus* is a primary neurocranial structure, as de Beer (1926: 332) had originally said.

The initial suggestion that the lateral commissure was of visceral origin was made by Allis (1914a), who maintained that in *Neoceratodus* it came from the mandibular arch. Holmgren (1940; 1943: 43) later claimed to have furnished complete evidence that the lateral commissure in sharks was derived from the mandibular arch. This evidence consists of a membranous connection between the postorbital process and the basiotic lamina in embryo *Squalus* (Holmgren 1940: fig. 67), a membranous connection between the same process and the hyomandibula in *Etmopterus* (Holmgren 1940: figs 81, 89) and between the postorbital process and the spiracular cartilages in *Raja* (Holmgren 1940: 184). In none of Holmgren's descriptions is there any indication of chondrification within this membrane, other than the formation of spiracular cartilages ventrally. Jollie (1971: 37) confirmed the mandibular arch origin of the lateral commissure in *Squalus*, even though he regarded the structure as a mandibular commissure, not as the lateral commissure proper, which he equated with part of the otic capsule unrelated to the jugular vein. Bertmar (1959: 314, 339) pointed out that while Allis's (1914a) deductions were founded on imperfect information in *Neoceratodus*, Holmgren (1940, 1943) had confused the lateral commissure of sharks with mandibular arch structures (see also Bjerring 1967: 262). However, Bertmar (1959: 314; 1963: 337) went on to suggest that the lateral commissure in *Neoceratodus* is derived from the hyoid arch and represents fused infra- and suprapharyngohyals, and thus added some credence to the theory of the hyal origin of the commissure in *Eusthenopteron* proposed by Jarvik (1954: 75).

The only possible confirmation of Bertmar's (1959) theory would be to show that the lateral commissure in selachians is of hyoid arch origin, which is exactly what Jollie (1971: 37) proposed. Unfortunately, Jollie homologized the lateral commissure of actinopterygians with the otical shelf of sharks, despite the fact that a lateral commissure exists in many selachians (*Oxynotus*, *Scymnodon*, *Centrophorus*, *Cladodus*; Holmgren 1940, 1941) and is massive in *Squatina* and many fossil sharks (*Xenacanthus*, *Tamiodontis*, *Hybodus*). Thus from the evidence presented by Holmgren (1940), El-Toubi (1949) and Jollie (1971) for *Squalus*, and Holmgren (1940) for *Etmopterus*, there is no reason to suppose that the lateral commissure in selachians forms in a manner significantly different from that in actinopterygians. Furthermore, although the lateral commissure is missing in hexanchoids, galeomorphs, many rays, torpedoes and chimaeroids, its presence in other selachians, osteichthyans, placoderms (Young 1980) and acanthodians (Miles 1973a: fig. 4) suggests it is a primitive feature of gnathostomes.

Allis (1914b, 1919) first introduced the term 'trigeminofacialis chamber' for the space in the side wall of the braincase of actinopterygians immediately in front of the auditory capsule. This

chamber is made up by the pars ganglionaris and the pars jugularis. Allis pointed out that the trigeminofacial chamber is single in *Amia* and *Lepisosteus* because the pars ganglionaris and pars jugularis are confluent, but that in *Scomber* and the scorpaenoid teleosts the chamber is divided. Goodrich (1930: 277), knowing that in selachians the trigeminal and facial ganglia are intramural, decided that the condition in *Amia* and *Lepisosteus*, in which an intramural recess (pars ganglionaris) is confluent with an extramural recess (pars jugularis), represents the basic configuration for actinopterygians. He further believed that in teleosts the trigeminofacial chamber is secondarily divided by a bony wall. This view was also held by de Beer (1937: 56, 428), who qualified it by pointing out that the trigeminofacial chamber of *Amia* could be derived from the condition in *Squalus* if the acustico-trigeminofacialis recess and the jugular canal of the latter 'were thrown into one'. Earlier (de Beer 1926), however, he had shown that the trigeminofacial chamber is separate from the jugular canal in the development of *Acipenser* and *Amia*.

In chondrichthyans the pars jugularis is separated from the pars ganglionaris by the lateral wall of the neurocranium (prefacial commissure), whereas the medial wall of the trigeminofacialis chamber (prefacial commissure + pila antotica) is invariably complete and ossified in palaeoniscids, fossil halecostomes, halecomorphs and all the major groups of teleosts. From this it is clear that the condition in *Amia*, *Lepisosteus* and certain advanced teleosts in which the prefrontal commissure and pila antotica fail to ossify, thereby allowing the chamber to communicate widely with the cranial cavity, is specialized.

Unlike chondrichthyans the facial and trigeminal ganglia are primitively extracranial in actinopterygians. This is certainly the case in palaeoniscids, *Polypterus*, *Acipenser*, caturids, *Lepidotes*, pholidophorids and early leptolepids, whereas in *Ichthyokentema*, Upper Jurassic leptolepids and primitive living teleosts the geniculate and gasserian ganglia are partly or wholly intracranial (Patterson 1975: 401). Schaeffer (1971: 7) attempted to reconcile the varying locations of the two ganglia in the jugular canal of different actinopterygian groups, by suggesting that the term 'trigeminofacialis chamber' be restricted to the extramural cavity between the lateral cranial wall and the lateral commissure. If we accept this simple definition then it is obvious that the trigeminofacialis chamber of primitive actinopterygians (palaeoniscids, *Polypterus*, *Acipenser*, etc.) is not very different from that of selachians such as *Oxynotus*, *Squatina* and *Squalus*. Since such a chamber is also found in placoderms (*Brindabellaspis*, Young 1980: fig. 10) it must be considered a primitive gnathostome character. Nevertheless, because the geniculate and gasserian ganglia have varied relationships to this extramural cavity (trigeminofacialis chamber) and to the mouth of the jugular canal in actinopterygians and selachians, it is necessary to establish the primitive condition in actinopterygians, osteichthyans and gnathostomes.

(a) ACTINOPTERYGIANS. In most palaeoniscids the lateral commissure is a massive endochondral structure formed by the prootic and penetrated by a long jugular canal. The commissure is also massive in *Polyodon* but is less extensive in *Polypterus*, *Acipenser*, *Mimia* and *Moythomasia* and is considerably reduced in *Amia*, *Lepisosteus*, parasemionotids, caturids, semionotids, pachycormids and pholidophorids. The lateral wall of the jugular canal in many palaeoniscids is perforated by several other canals; a ventral one which transmitted the orbital artery, and one or more dorsal foramina which transmitted the hyomandibular trunk or its branches, or both. Actinopterygians with three separate posterior openings (for the jugular vein, orbital artery and hyomandibular trunk) include *Pteronisculus*, *Kentuckia*, *Kansasiella*, *Perleidus*, leptolepids and other primitive teleosts. Patterson (1975: 400), however, has demonstrated that the condition in teleosts is secondary and developed as a result of extensive membrane bone outgrowths.

The jugular canal may open posteriorly by a single foramen transmitting the jugular vein, orbital artery and hyomandibular trunk as in *Mimia*, *Acipenser*, parasemionotids, caturids, pachycormids, *Lepidotes*, *Lepisosteus*, *Dapedium* and pholidophorids; or the orbital artery may enter by a separate vertical canal as in *Kansasiella*, *Moythomasia*, *Boreosomus*, *Australosomus*, *Pteronisculus cicatrosus*, *Saurichthys*, *Polyodon* and *Amia*; or the orbital artery may pass outside the commissure as in *Polypterus*.

The facial canal, which primitively transmitted only the palatine and hyomandibular trunk of the

facial nerve, opens into the ventromedial corner of the orbital opening of the jugular canal in *Pteronisculus*, *Mimia*, *Moythomasia*, *Kentuckia*, *Boreosomus*, *Saurichthys*, *Perleidus* and parasemionotids and the geniculate ganglion lay in the floor of the jugular canal. In *Acipenser* the facial canal emerges in the orbit and the hyomandibular trunk turns posteriorly to traverse the jugular canal.

In *Polypterus* and *Kansasiella* the facial canal opens into the middle of the jugular canal and the geniculate ganglion lay within the jugular canal.

In caturids, *Lepidotes*, pachycormids and pholidophorids, where the lateral commissure is reduced, the facial canal opens just behind the jugular canal.

The lateralis branches of the facial nerve issue through the trigeminal foramen in palaeoniscids, pholidophorids, pachycormids, leptolepids and other teleosts, and in most of these fishes the external opening of the trigeminal canal lies anterodorsal to the facial foramen, in the upper part of the orbital opening of the jugular canal. In *Polypterus* there is a separate lateralis ganglion (lateralis—communis of Allis 1922: 274) dorsal to the trigeminal ganglion. This lateralis ganglion is partly extracranial and partly intracranial and is continuous with the intracranial portion of the facialis ganglion. In *Amia* a similar lateralis ganglion lies above the gasserian ganglion. In *Polyodon* and *Acipenser* the lateralis branches of the facial nerve emerge into the orbit through separate foramina (superficial ophthalmic and otic branches). This is considered to be a specialization following loss of the prefacial commissure in *Acipenser*. Both caturids and *Amia* have an intramural canal for the superficial ophthalmic nerves, and in *Ospia* and some parasemionotids the trigeminal canal is divided by a horizontal partition, with the superficial ophthalmic nerves passing out separately through the dorsal part (Patterson 1975: 405).

In the Gogo palaeoniscids there is a separate foramen dorsal to the facial canal and posterolateral to the trigeminal canal. Although no such foramen or canal has been reported in any other actinopterygian, by comparison with *Polypterus* and *Amia* this foramen must have transmitted the lateralis branches of the facial nerve.

The facial and trigeminal canals originate in front of the recess for the utriculus in *Mimia*, *Moythomasia*, *Pteronisculus*, *Australosomus*, and pholidophorids, but in *Mimia* a bridge of bone separates the facial canal from the lateralis canal and the latter originates in the most anterior part of the utricular recess. In many other palaeoniscids such as *Kansasiella*, *Kentuckia* and *Boreosomus*, and in *Perleidus* and fossil and living neopterygians (parasemionotids, *Caturus*, *Lepidotes*, *Dapedium*, *Amia*, *Lepisosteus*), the facial and trigeminal canals originate in the utricular recess. This is considered a specialization (Patterson 1975: 408).

In *Mimia* and all previously described palaeoniscids, chondrosteans, perleidids and pholidopleurids (*Pteronisculus*, *Kentuckia*, *Kansasiella*, *Acipenser*, *Polyodon*, *Boreosomus*, *Birgeria*, *Perleidus*, *Australosomus*) the facial canal opens into the orbital opening of the jugular canal (but see Lehman 1969), the geniculate ganglion lay in the floor of the canal, the palatine nerve passed down into the parabasal canal along the hind wall of the orbit, and there is no prefacial (prepalatine) floor to the jugular canal. This is also the condition in parasemionotids, *Lepisosteus* and *Amia* except that in some of the more fully ossified specimens of parasemionotids (Patterson 1975: 405) there are rudiments of a prepalatine strut.

In *Moythomasia*, however, the external opening of the facial canal is confluent with a palatine fenestra, a rather large opening in the floor of the jugular canal. Thus *Moythomasia* is the only palaeoniscid so far described with a prefacial floor to the jugular canal. This prefacial floor has the same proportions as in *Pholidophorus* and *Pachycormus* (Patterson 1975: 404; fig. 64) and the geniculate ganglion must have lain within the palatine fenestra. In *Lepidotes*, *Dapedium*, *Leptolepis* and many living teleosts the opening in the floor of the jugular canal decreases in size so that only a palatine foramen remains. The palatine nerve passed through this opening into the myodome and the geniculate ganglion must have lain in the extramural space in the floor of the jugular groove.

In most caturids (*Heterolepidotus*, '*Aspidorhynchus*', *Caturus*, *Macrepistius*) the prepalatine floor is represented by a slender strut, but in the *Caturus* described by Rayner (1948: fig. 5) the floor is more complete and similar to that in *Moythomasia* and *Pholidophorus*.

The otic nerve canal originates in the wall of the orbit above the opening of the jugular canal in

Mimia, *Moythomasia*, *Kansasiella*, *Perleidus*, *Polypterus*, parasemionotids, *Dapedium*, *Lepidotes*, *Pachycormus* and *Pholidophorus*, but in *Pteronisculus*, *Kentuckia*, *Boreosomus*, *Australosomus*, *Heterolepidotus*, *Caturus*, *Macrepistius*, *Amia* and *Lepisosteus* it originates in the roof of the mouth of the canal. The otic nerve canal passes through the postorbital process to join the spiracular canal in *Boreosomus*, *Australosomus*, *Lepidotes*, *Pachycormus*, and *Pholidophorus*, while in *Kansasiella* (Poplin 1974: fig. 12) it is only just excluded from the top of the spiracular canal. But in *Pteronisculus*, *Kentuckia*, *Saurichthys*, *Acipenser*, parasemionotids, *Dapedium*, *Heterolepidotus*, *Lepisosteus* and *Amia* the otic canal opens into the floor of the fossa bridgei, medial to the spiracular canal. In larval *Amia* (Goodrich 1930: fig. 733) the otic nerve passes into the top half of the spiracular canal and not into the fossa bridgei, and in *Polypterus* the otic nerve perforates the postorbital process, passes beneath the ampulla of the anterior semicircular canal and emerges on the roof of the neurocranium medial to the most anterior portion of the spiracle. In *Mimia* and *Moythomasia* the otic nerve canal similarly passes through the postorbital process medial to the spiracular groove.

The superficial ophthalmic nerves are believed to have emerged through the trigeminal foramen in palaeoniscids, *Perleidus*, *Dapedium*, *Lepidotes*, *Pachycormus* and *Pholidophorus*. In *Moythomasia* there is a short canal leading upwards from the roof of the recess for the trigeminal and lateralis ganglia. This canal passes up through the wall of the orbit (pterosphenoid pedicel) and must have served for the superficial ophthalmic nerves. Loss of the separate lateralis canal and enlargement of the external opening of the trigeminal canal would lead to the condition seen in *Kentuckia*, *Ospia*, caturids and *Amia*.

There is a separate profundus foramen in *Mimia*, *Moythomasia*, *Kentuckia*, *Kansasiella*, *Pteronisculus*, *Perleidus*, parasemionotids, caturids, *Lepidotus*, *Lepisosteus*, *Dapedium*, *Pachycormus*, pholidophorids and the Sinemurian *Leptolepis*, but in all other leptolepids there is no separate profundus foramen. In some living teleosts there is a separate profundus foramen, but in many others the nerve enters the orbit through the oculomotor foramen, as in *Polypterus*. There is no sign of a profundus foramen in *Boreosomus*, *Saurichthys* or *Australosomus* and there is no separate foramen in *Amia*. From this evidence it is not clear whether a separate profundus foramen is primitive. In *Mimia* the root of the profundus, together with the trigeminal nerve, passed into the base of the trigeminal canal. The trigeminal canal immediately divides and the profundus passed forwards and downwards to enter the orbit through a separate foramen. The condition in *Boreosomus*, *Saurichthys* and *Australosomus* could be derived from that in *Mimia* merely by enlargement of the trigeminal canal, so that the profundus emerged with the trigeminal nerve (see also Nielsen 1949: 58), as in selachians.

From this survey I conclude (as did Patterson 1975: 408) that primitively in actinopterygians the lateral commissure was massive and that the posterior lateral wall of the jugular canal was perforated by the hyomandibular trunk dorsally and the orbital artery ventrally. The extracranial gasserian and geniculate ganglia lay in the mouth of the orbital opening of the jugular canal and the facial and trigeminal canals originated in front of the utricular recess. The facial canal transmitted the palatine nerve and hyomandibular trunk, with the latter turning posteriorly to traverse the jugular canal and with the palatine nerve passing into the parabasal canal. The trigeminal canal opened into the orbit dorsomedial to the facial canal and the otic nerve canal originated in the wall of the orbit above the jugular canal and passed up onto the roof of the neurocranium medial to the spiracle.

(b) OSTEICHTHYANS. In actinistians the lateral commissure is well developed (*Nesides*, Bjerring 1977: fig. 23a; *Macropoma*, *Latimeria*, Millot & Anthony 1958) and is similar to that in the Gogo palaeoniscids. The jugular canal is long and transmits the hyomandibular trunk, orbital artery and jugular vein in *Latimeria*. In rhipidistians such as *Eusthenopteron* (Jarvik 1954: fig. 1), *Ectosteorhachis* (Romer 1937: fig. 2), *Porolepis* (Bjerring 1967: 224) and *Glyptolepis* (Jarvik 1972: fig. 21) the lateral commissure is also massive and the jugular canal is similar in length to that in palaeoniscids and actinistians. The lateral commissure is not easily recognizable in adult dipnoans owing to fusion of that region with the palatoquadrate, but Bertmar (1963: 337) believed it can readily be distinguished in embryos of *Neoceratodus*. A long jugular canal is

present and transmits the hyomandibular trunk, jugular vein and orbital artery, as in many actinopterygians. In the Devonian dipnoans *Griphognathus* and *Holodipterus* there are separate posterior openings (Miles 1977: figs 14, 44) for these three structures, as in primitive actinopterygians, but in *Chirodipterus* there are two, one for the jugular canal and the other for the hyomandibular trunk and the orbital artery, while in the Recent *Neoceratodus* there is a single posterior opening for all three structures.

In some actinistians (*Nesides*, *Latimeria*) the opening of the facial canal lies in front of the jugular canal, but in *Rhabdoderma* and the rhipidistians *Ectosteorhachis*, *Eusthenopteron*, *Glyptolepis* (Jarvik 1972: fig. 21) and *Youngolepis* (Chang 1982: 51) the facial canal opens into the mouth of the jugular canal much as in palaeoniscids.

In the Devonian dipnoan *Griphognathus* (Miles 1977: fig. 53) the root of the facial nerve opens into the centre of the jugular canal, but the anterior part of the jugular canal is considered a dipnoan specialization, formed by fusion of the ascending process of the palate to the pila antotica. The facial and trigeminal ganglia were extracranial as in *Neoceratodus*.

In *Latimeria* (Millot & Anthony 1958) the gasserian and geniculate ganglia are separate and intramural, the geniculate ganglion lies between the two moieties of the braincase, and there is no separate lateralis canal. In fossil actinistians such as *Diplocercides* they may also be assumed to have been intracranial.

In rhipidistians such as *Ectosteorhachis* (Romer 1937: fig. 2) and *Eusthenopteron* (Jarvik 1954: fig. 1A; Bjerring 1971: fig. 9) the facial and trigeminal ganglia appear to have been intracranial.

The trigeminal, facial and lateralis canals arise in front of the recess for the utriculus in the dipnoans *Griphognathus* and *Chirodipterus* (Miles 1977: figs 10, 17) and all the branches of the trigeminal and facial nerves appear to originate well in front of the utricular recess in *Eusthenopteron* (Jarvik 1975: fig. 14) and *Ectosteorhachis* (Romer 1937: figs 8, 13). The otic canal originates above the jugular canal in the actinistians *Latimeria*, *Nesides*, *Rhabdoderma* and *Laugia* and the rhipidistians *Eusthenopteron*, *Ectosteorhachis*, *Rhizodopsis* and *Glyptolepis*. The otic nerve canal originates behind the spiracular groove in *Eusthenopteron* (Jarvik 1954: fig. 1, spic) and opens into the anterior portion of the post-temporal fossa. In *Youngolepis* (Chang 1982: fig. 15A, r.ot.l) the otic nerve ran in a groove (anterodorsal to the lateral commissure) which terminates below the temporal sensory canal. In *Latimeria* the otic nerve passes up behind the spiracle.

A separate canal for the superficial ophthalmic nerves is found in *Griphognathus* (Miles 1977: figs 10, 33, 55, VIIs?) and *Chirodipterus* (Miles 1977: figs 21, 35, 38, VI?). In *Diplocercides* (Bjerring 1971; 1977: fig. 23A) a somewhat smaller foramen above the facial canal must have also served for the lateralis branches of the facial nerve. The lateralis root in *Latimeria* exits through the intracranial joint.

There is a separate profundus canal in actinistians and Devonian dipnoans. In actinistians (*Latimeria*, *Rhabdoderma*, *Macropoma*, *Nesides*) it is within the 'basisphenoid', but in *Chirodipterus* (Miles 1977: figs 17, 47) its origin is just in front of the trigeminal canal and above the prootic bridge (as in palaeoniscids).

Thus from this brief summary I conclude that the osteichthyan morphotype must have been similar to the actinopterygian one outlined above, apart from the path of the otic nerve canal.

(c) GNATHOSTOMES. In primitive sharks such as *Hybodus* (BMNH P.50869, Maisey 1983) and *Xenacanthus* (Schaeffer 1981: fig. 6) the lateral commissure is a massive structure of calcified cartilage penetrated by a long jugular canal much as in *Polyodon*, but only the jugular vein and hyomandibular trunk passed through it. In *Xenacanthus*, *Cladodus* and *Squalus*, the hyomandibular trunk exits through a separate foramen. In many other selachians such as *Scymnodon* and *Oxynotus* the hyomandibular trunk exits from the skull posterior to the jugular canal and does not pass through it; this is considered specialized and related to the posterior position of the hyomandibula. A lateral commissure is also clearly recognizable in pristiophorids, some rhinobatoids (Compagno 1977: 310, 316) and *Squatina* (Holmgren 1941: 36). The orbital artery never passes through the jugular canal or the lateral commissure; instead

it often pierces the subotical shelf (cf. *Squalus*). The palatine nerve, on the other hand, may pierce the basal part of the lateral commissure (*Tamiobatis*, *Xenacanthus*, *Squalus*).

The facial canal is variable in position in selachians. In *Scymnorhinus* the facial canal opens into the middle of the jugular canal as in *Polypterus* (except that the ganglion is intramural), but in *Rhinobatus*, where the lateral commissure is reduced, the facial canal opens in front of the jugular canal and in *Etmopterus* and *Squatina* it opens into the ventromedial corner of the orbital opening of the jugular canal, as in many palaeoniscids and parasemionotids.

In most selachians the lateralis branches of the facial nerve issue through the trigeminal foramen, as in actinopterygians, and the trigeminal foramen often lies in the orbital opening of the jugular canal (*Oxynotus*, *Scymnodon*, *Xenacanthus*, *Tamiobatis*, *Cladodus*, *Hybodus*). In other selachians (*Etmopterus*, *Squatina*, *Rhinobatus*) the trigeminal foramen opens in front of the jugular canal. The gasserian and geniculate ganglia are always intracranial. The otic nerve canal passes from the orbit up through the postorbital process to open on the roof of the neurocranium medial to the spiracle in *Chlamydoselachus* and *Heterodontus*, and there is a separate foramen for the profundus.

A massive lateral commissure is also found in Devonian placoderms such as *Brindabellaspis* and *Buchanosteus* (Young 1979; 1980: figs 8, 9) and the jugular canal is longer proportionally than in primitive actinopterygians. The hyomandibular trunk passed out through the anterior opening of the jugular canal in *Brindabellaspis*, but passed across the canal (at right angles to it) in *Buchanosteus*. The orbital artery entered the jugular canal by a separate foramen in *Kujdanowiaspis* (Young 1979: 329), but in *Buchanosteus* (Young 1979: fig. 9) it passed lateral to the jugular canal and in *Brindabellaspis* (Young 1980: 41) medial to it.

The facial canal seems to be less variable in position in placoderms than selachians. In *Brindabellaspis* and *Wijdeaspis* (Young 1978, 1980) it opens into the mouth of the jugular canal, but in *Buchanosteus* (Young 1979) the facial canal opens into the anterior half of the jugular canal. There is a separate profundus canal in *Jagorina*, *Brindabellaspis* and *Macropetalichthys* and a separate canal for the superficial ophthalmic nerves in *Buchanosteus* (Young 1979: fig. 5).

In *Acanthodes* the lateral commissure is not really discernible because of lack of ossification in that region, but a short perichondral commissure is present as Miles (1973a: fig. 4) presumed (BMNH specimens).

From this brief survey I conclude that the primitive gnathostome possessed a long lateral commissure with separate openings for the jugular vein and hyomandibular trunk; the facial canal emerged in the orbital opening of the jugular canal and the trigeminal canal dorsomedial to it; the otic nerve canal originated in the posterior wall of the orbit and passed up to the neurocranial roof medial to the spiracle.

5. Hyomandibular facet. In the Gogo palaeoniscids this lies obliquely between the sphenotic and opisthotic with the prootic forming a small portion of the ventral margin. A similar oblique facet above the jugular canal is characteristic of most palaeoniscids, *Polyodon*, *Acipenser*, *Polypterus*, etc.

In later actinopterygians such as amioids, semionotids, pachycormids, pholidophorids and Recent teleosts the facet has become more or less horizontal. In amioids, pholidophorids and pachycormids it lies between the sphenotic and prootic anteriorly and the pterotic and opisthotic posteriorly (except in *Amia* and semionotids), while in leptolepids and many other teleosts the posterior end lies entirely within the pterotic. There is a single hyomandibular articulation in actinopterygians and the oblique facet in palaeoniscids is considered primitive.

In actinistians the hyomandibular articulation is a very large, bilobed, cartilage-capped area (*Nesides*, Bjerring 1977: fig. 23; *Rhabdoderma*, Forey 1981: fig. 1; *Latimeria*, Millot & Anthony 1958) which straddles the jugular canal obliquely and lies between the prootic and opisthotic. In rhipidistians (*Eusthenopteron*, Jarvik 1954: fig. 1; *Ectosteorhachis*, Romer 1937: fig. 2; *Porolepis*, Bjerring 1967: 224; *Youngolepis*, Chang 1982: fig. 15A) the articulation is double, oblique and crosses the jugular canal. I assume it lies between the prootic and opisthotic in *Eusthenopteron*. The hyomandibular facet in Devonian dipnoans straddles the jugular canal obliquely, as in actinistians and rhipidistians (Miles 1977: 90), and the articulation is divided into dorsal and

ventral areas by a thin tract of perichondral bone. Despite the arguments of Miles (1977: 91) I see no reason to change my previous view (Gardiner 1973: 109, 122) that the hyomandibula has a double articulation with the neurocranium in Devonian dipnoans, much as in rhipidistians. In Recent dipnoans the facet is lost.

In *Acanthodes* (Miles 1964: fig. 1B) the head of the hyomandibula is presumed to have lain obliquely between the perichondral lateral commissure and otic ossification and dorsal to the jugular canal, as in actinopterygians.

In chondrichthyans the condition is variable. In *Heptanchus*, *Squatina* (Holmgren 1941: 30) and *Cobelodus* (Zangerl & Case 1976) the hyomandibular facet is set obliquely across the posterior part of the auditory region and in *Mustelus*, *Carcharinus* and *Heterodontus* (Holmgren 1941: 45) the articulation is on the anterior half of the auditory region. In *Chlamydoselachus* and *Orectolobus* the hyomandibular facet is a long, broad groove dorsal to the auditory bulla, whereas in *Squalus* it is below and behind the bulla. In *Rhinobatus*, *Raja*, *Discobatus*, *Pristis*, *Pristiophorus*, *Dasybatus* (Holmgren 1941) and all other rays the articulation is divided into two facets which are situated in the posterior part of the auditory region. In all these Recent sharks and rays without exception the hyomandibula articulates with the endocranium ventral to the jugular vein, and usually below the ridge for the horizontal semicircular canal, and is suspensory. This ventral position of the hyomandibula with respect to the jugular vein in selachians has generated much argument as to whether the condition is primitive (Holmgren 1943: 102, 104) or advanced (Gardiner 1973: 122), while its posterior position has been responsible for the development of elaborate theories of the incorporation of hyoid arch material (pharyngohyal) into the auditory capsule (Holmgren 1940; 1943: 43, 68), to form the otical shelf and hyomandibular facet in rays. Jarvik (1954: 75) has used this supposed evidence of incorporation of the hyoid arch material into the auditory capsule of selachians to support a similar presumed incorporation of hyoid arch material into the lateral commissure and 'otical shelf' region of *Eusthenopteron*. However, the supposed incorporation of hyoid material in sharks and rays described by Holmgren (1940, 1943) always occurs posterior to the lateral commissure (Holmgren 1940: fig. 130), whereas the 'otical shelf' of *Eusthenopteron* (Jarvik 1954: fig. 1A) lies anterior to the lateral commissure. But the discovery in *Tristychius* (Dick 1978) and *Hybodus* (Maisey 1982, 1983) of a hyomandibula which articulated with the braincase above the jugular canal as in actinopterygians, actinistians and rhipidistians suggests that it is no longer worth while to invoke theories of hyoid arch incorporation to explain the 'otical shelf' in selachians.

In those placoderms in which the hyomandibular articulation has been described in detail (Young 1980, Stensiö 1963a, Goujet 1975) it is at the base of the lateral commissure (*Brindabellaspis* Young 1980) and in front of the foramen for the hyomandibular trunk.

I conclude that primitively in gnathostomes the hyomandibula must have articulated with the braincase in the region of the lateral commissure and was suspensory. Whether the articulatory facet is above or below the jugular canal seems of little significance and there is no reason to suppose that the hyomandibular-neurocranial attachment developed more than once.

6. *Otico-sphenoid fissure*. This has so far only been reported in the Gogo palaeoniscids. It was cartilage-filled and separates the anteroventral corner of the prootic from the basisphenoid. It appears to correspond with the gap between the lateral commissure and the polar cartilage – trabecular bar of the embryo actinopterygian (Gardiner & Bartram 1977: 241). Together with the ventral otic fissure it is homologous with the ventral part of the intracranial joint of actinistians and rhipidistians (Gardiner & Bartram 1977: 242). However, this homology has been denied by Bjerring (1978).

7. *Fossa bridgei and lateral cranial canal*. The Gogo palaeoniscids resemble *Boreosomus* (Nielsen 1942) in the considerable variation shown in the degree of ossification of the dorsal otic region. In some specimens of *Mimia* (Fig. 12) there is large lateral cranial canal in the roof of the otic region occupying the whole of the area between the posterior and anterior semicircular

canals. This chamber is roofed by a sutureless skin of perichondral bone and connects with the cranial cavity posteriorly by a large opening through the loop of the posterior semicircular canal (Fig. 26). Anteriorly it may occasionally connect with the cranial cavity in front of the sinus superior by various small foramina. The supratemporal branch of the glossopharyngeal nerve enters the canal laterally. The spiracular groove lies anterolateral to the canal and is not included within it. In other specimens of *Mimia*, the lateral cranial canal is little more than a pocket in front of the posterior semicircular canal, but still maintains its posterior connection with the cranial cavity by a large foramen through the loop of the semicircular canal much as in *Kansasiella* (Poplin 1974: fig. 20, e.l.m, y) and *Kentuckia* (Rayner 1951: fig. 9, x).

The presence of a lateral cranial canal is considered to be a specialization of actinopterygians (Gardiner 1973: 113). Jarvik (1980) has shown that in Recent chondrosteans and holosteans there is a hemopoietic organ dorsal to the medulla which in *Lepisosteus* has earlike lobes passing forwards and upwards into the lateral cranial canal.

The Gogo palaeoniscids have no fossa bridgei, which if present would have overlain (in part) the lateral cranial canal. A lateral cranial canal is well developed in *Kentuckia* but the fossa bridgei is poorly defined and consists of several irregular cavities (Rayner 1951: figs 6, 9). Most palaeoniscids possess both a lateral cranial canal and a fossa bridgei, but the absence of the latter in the Gogo palaeoniscids is considered primitive.

In *Polypterus* there is neither a fossa bridgei nor a lateral cranial canal and this is considered primitive for osteichthyans. Actinopterygians in which the fossa bridgei and lateral cranial canal are separate include *Kansasiella*, *Boreosomus*, *Pholidophorus* (Patterson 1975: 336), *Leptolepis* (Patterson 1975: fig. 73), *Caturus* (Rayner 1948: fig. 9), *Heterolepidotus*, *Dapedium*, *Lepidotes*, parasemionotids and *Lepisosteus* (Gardiner 1973: 13). In many other actinopterygians there is a connection between the deeper, posterior part of the fossa bridgei and the cranial cavity (Nielsen 1942: 294; Patterson 1975: 392, 414). These connections are topographic homologues of parts of the lateral cranial canal. Forms in which the fossa bridgei communicates posteriorly with the cranial cavity by way of the lateral cranial canal include *Pteronisculus*, some specimens of *Boreosomus*, and *Polyodon* (cf. *Boreosomus* Nielsen 1942: fig. 59, where in one individual the fossa bridgei is separated by bone from the lateral cranial canal on one side, but on the other the two cavities are connected).

In several other actinopterygians (*Ospia*, *Acipenser*) where the lateral cranial canal and fossa bridgei have become confluent the lateral cranial canal portion has lost its connection with the cranial cavity; this is also considered to be a specialization. The lateral cranial canal communicates with the cranial cavity posteriorly through the loop of the posterior semicircular canal in the Gogo palaeoniscids, *Kansasiella* (Poplin 1974: fig. 22), *Kentuckia*, *Boreosomus* and *Polyodon*, but in caturids (*Caturus*, *Heterolepidotus*) and pholidophorids the canal has both anterior and posterior openings into the cranial cavity and in *Perleidus* there is only an anterior opening (Patterson 1975: 414). In leptolepids, *Lepisosteus* and *Lepidotes* the lateral cranial canal has lost the inner wall and thus has the form of a posterodorsal diverticulum of the cranial cavity (Patterson 1975: 413). In *Polyodon* the connection between the fossa bridgei and the cranial cavity, by way of the lateral cranial canal, is fat-filled.

The spiracular groove in the Gogo palaeoniscids and the spiracular canal in *Kentuckia* lie lateral to the area occupied by the fossa bridgei in other forms, and in *Polypterus* the spiracle lies alongside the braincase in the adult. The spiracle also lies freely alongside the intracranial joint in *Latimeria*. In *Eusthenopteron* Jarvik (1954: fig. 1A, spic) has claimed that a spiracular canal enters the fossa bridgei. However, the 'fossa bridgei' in *Eusthenopteron* is more reasonably interpreted as a post-temporal fossa and the 'spiracular canal' as the otic nerve canal. Subsequent evolution within actinopterygians brought about the formation of the spiracular recess (often called 'fossa bridgei anterior', Nielsen 1942: fig. 11) containing a blind-ending spiracular diverticulum in *Acipenser*, *Polyodon* and *Amia*. The recess is confluent with the fossa bridgei (Gardiner 1973: 114) in these fishes. In the Gogo palaeoniscids the spiracular groove is entirely outside the sphenotic, but in halecomorphs and pholidophorids the spiracular canal penetrates the postorbital process at the junction between the sphenotic and prootic (Patterson 1975: 399). The condition in which the fossa bridgei includes the spiracular recess but is still

roofed by dermal bone is met with in *Polyodon*, *Boreosomus*, *Perleidus*, *Acipenser*, *Ospia*, parasemionotids, caturids and pholidophorids.

In *Amia* and *Lepisosteus* the fossa bridgei is represented by an elongate pocket or groove, containing no musculature, which extends anteriorly to the opening of the spiracular canal. An area medial to the anterior semicircular canal in *Pholidophorus*, referred to as the antero-medial portion of the fossa bridgei by Patterson (1975), has no homologue in the Gogo palaeoniscids and is presumably a specialization of later actinopterygians.

In parasemionotids and primitive pholidophorids, behind the fossa bridgei and separated from it by a wall of bone, there is a small post-temporal fossa which probably contained trunk musculature (Patterson 1975: 392). In Upper Jurassic pholidophorids the post-temporal fossa and fossa bridgei have become confluent, by the breakdown of the intervening wall, allowing the axial muscles to extend into the fossa bridgei, as in Recent teleosts (Patterson 1975: 392). There is no homologue of the post-temporal fossa in palaeoniscids, but a rudimentary post-temporal fossa appears to be present in *Birgeria*, *Perleidus*, *Saurichthys*, and sturgeons (Griffith & Patterson 1963: 35; Patterson 1975: 392). The post-temporal fossa is presumed to be a specialization of later actinopterygians, and Patterson (1975: 393) has shown how the pre-epiotic pocket of primitive teleosts is the topographic homologue of the posteromedial portion of the fossa bridgei of pholidophorids and primitive leptolepids. A further small blind-ending fossa (wrongly referred to as a pre-epiotic fossa by Gardiner, 1973: 113) which runs down under the posterior semicircular canals in the clupeid *Alosa* (Todd 1973) is possibly the homologue of the lateral cranial canal of *Pholidophorus*.

There is no evidence of a fossa bridgei in *Latimeria* or any fossil actinistian (including *Nesides*). A small post-temporal fossa is present in some later actinistians and receives trunk muscles in *Latimeria*; this must have developed in parallel with that in later actinopterygians and rhipidistians (see below).

A well-developed post-temporal fossa is also present in many rhipidistians, and in *Eusthenopteron* (Jarvik 1954; 1975: figs 8, 9, 11, 13; fossa bridgei) it is roofed by dermal bone. It lies between the posterior and anterior semicircular canals and is limited laterally by the parotic crista which encloses the external semicircular canal. It is in a similar position to the posterior part of the fossa bridgei and the lateral cranial canal in palaeoniscids. Presumably it was invaded by axial muscles much as in later actinopterygians, actinistians and tetrapods. A similar post-temporal fossa is found in *Ectosteorhachis*, *Rhizodopsis*, *Osteolepis* and *Glyptolepis*.

In Devonian dipnoans, according to Miles (1977: 74), there is a fossa comparable to that in rhipidistians, the masseter fossa. It is limited laterally by the parotic crista (which encloses the external semicircular canal), roofed by dermal bone, and extends medial to the posterior vertical semicircular canal; the fossa is open posteriorly. However, since the fossa in Devonian dipnoans is presumed to have housed only the adductor mandibulae (cf. *Neoceratodus*) it may not be homologous with the rhipidistian post-temporal fossa as Miles assumed. Moreover, although a post-temporal fossa is present in many amphibians (loxommatids) it is missing in primitive temnospondyls, anthracosaurs and other primitive amniotes.

The fossa bridgei is recognizable only in later actinopterygians and its absence is considered a primitive osteichthyan feature. There is no indication of a fossa bridgei or a post-temporal fossa in acanthodians, placoderms or chondrichthyans.

8. *Spiracle and spiracular canal.* In the Gogo palaeoniscids the spiracular groove is long and the spiracle was open. However, in some specimens of *Moythomasia* the groove is embraced dorsally by a thin ring of bone (Fig. 83) similar to that described in *Eusthenopteron* (Jarvik 1954: fig. 1B, b.al). The spiracle opened dorsally through a slit in the dermal roof. In *Polypterus* the anterior edge of the spiracular pouch lies in the fossa spiracularis (Allis 1922: 193) and the spiracle opens through a slit between the 'parietal' and two spiracular ossicles.

In *Acipenser*, *Polyodon* and *Lepisosteus* the spiracular pouch divides into two tubes, one of which opens on the skull roof (spiracle) and the other forms the blind-ending spiracular canal. In *Amia* only the blind-ending spiracular canal remains. A homologous spiracular canal penetrates the postorbital process of most palaeoniscids and other primitive actinopterygians. The

spiracular canal is still relatively short in *Pteronisculus*, *Kansasiella* and *Kentuckia* and is presumed to be contained within the sphenotic. The canal is proportionally longer in *Boreosomus*, *Birgeria*, *Perleidus*, *Australosomus*, *Acipenser* and *Polyodon*, but in these last two living chondrosteans it is housed in cartilage.

A spiracular canal (or dorsal diverticulum) is found in many selachians where it is contained within the ventrolateral wall of the auditory capsule, below the external semicircular canal. Another more ventromedial diverticulum houses a spiracular sense organ. This dorsal or auditory diverticulum of sharks is directed towards the ventral wall of the auditory 'capsule' whereas that of *Acipenser*, *Lepisosteus* and *Amia* passes up along side the trigeminofacialis chamber before piercing the postorbital process. From this evidence and from the fact that in *Latimeria* the spiracle was also unenclosed and without a diverticulum, the condition in the Gogo palaeoniscids, *Polypterus* and *Latimeria* is considered primitive for osteichthyans. Subsequent evolution within the actinopterygians led towards elongation of the enclosed portion of the spiracular canal at the expense of the spiracular groove (Patterson 1975: 399) and the spiracular canal came to open within the fossa bridgei (Gardiner 1973: 113). A long spiracular canal is found in parasemionotids, caturids (*Caturus*, Rayner 1948: fig. 5; *Heterolepidotus*, Patterson 1975: fig. 102; '*Aspidorphynchus*', Patterson 1975: fig. 99), amiids (*Sinamia*, Stensiö 1935; *Enneles*, Santos 1960), semionotids (*Dapedium*, Patterson 1975: fig. 112; *Lepidotes*, Patterson 1975: fig. 108), pachycormids (*Pachycormus*, Patterson 1975: fig. 106), pholidophorids and Lower Jurassic leptolepids, but it is obliterated in later leptolepids and living teleosts (Gardiner 1973: 111; Patterson 1975: 398).

Living chondrosteans and holosteans have a neuromast organ lodged near the top of the spiracular canal, supplied by the otic branch of the facial nerve. A similar neuromast sense organ occurs in selachians (Wright 1885), but here it is lodged in a closed vesicle which has become pinched off from the base of the spiracular cleft.

In *Latimeria* the spiracle lies free alongside the intracranial joint. It is closed dorsally and terminates just beneath the dermal roof. As in *Polypterus* (and holocephalans) there is no spiracular sense organ, but the overlying neuromast of the temporal canal is greatly enlarged (Forey, personal communication).

Eusthenopteron is the only rhipidistian in which there is clear evidence of a spiracular groove (Jarvik 1954: fig. 22, gr. psp.). The spiracle in lungfishes is rudimentary and no trace of it has been described in fossil dipnoans (Gardiner 1973: 113; Miles 1977). A spiracular sense organ (Pinkus' organ), however, is found in Recent dipnoans where it is lodged in the otic process of the palatoquadrate, and a deep fissure in front of the hyomandibular facet in Devonian dipnoans (Miles 1977: 79) may have housed a similar sense organ.

It is thus apparent that a bone-enclosed spiracular canal and sense organ is a synapomorphy of advanced actinopterygians, whereas the presence of the sense organ may be more general (selachians, later actinopterygians and dipnoans).

9. *Origin of dorsal hyoid constrictor muscle.* In living chondrosteans there is an undifferentiated dorsal hyoid constrictor which forms a continuous sheet of muscle and originates along the dorsolateral margin of the braincase from hyomandibular facet to auditory capsule. It inserts ventrally on the hyomandibula and opercular.

A similar constrictor hyoideus dorsalis is found in selachians and its dorsal portion inserts on the hyomandibula (Edgeworth 1935: 98). From this evidence we can assume that primitively in gnathostomes the hyomandibula was levated from above by the anterodorsal portion of the hyoid constrictor.

In the development of *Polypterus*, *Amia* and *Lepisosteus* the anterior edge of the hyoid constrictor spreads forwards internal to the hyomandibula to form the adductor hyomandibulae, and the posterior portion of the constrictor differentiates into the adductor operculi. In *Amia* and teleosts the constrictor hyoideus is still more elaborately differentiated. If *Polypterus* is the sister-group of the chondrosteans plus neopterygians then the adductor hyomandibulae must have evolved separately in at least two lines of Recent fishes. *Latimeria* (Millot & Anthony

1965), in which the adductor operculi lies dorsal to the adductor hyomandibulae, suggests yet another separate origin.

In the Gogo palaeoniscids there is a continuous dorsal muscle scar stretching from just behind the point of articulation of the hyomandibula to the occipital fissure, only interrupted by a groove for branches of the glossopharyngeal and vagus nerves. It is presumed that this elongate area gave rise to an undifferentiated dorsal hyoid constrictor muscle as in living chondrosteans. It is unlikely that any part of the dorsal hyoid constrictor had its origin in the conspicuous 'subtemporal fossa' (Gardiner 1973: fig. 3) as suggested by Patterson (1975: 395), since the whole of this fossa consists of fenestrated bone, totally unsuitable for muscle origin. This so-called 'subtemporal fossa' in the Gogo palaeoniscid results from the lack of ossification of the side wall of the braincase in the neighbourhood of the jugular vein and is not such a distinct feature as in pholidophorids and other teleosts. There is no obvious subtemporal fossa in any other palaeoniscid, living chondrostean or *Polypterus*, and in the latter fish the adductores hyomandibulae and operculi form a continuous muscle (Lauder 1980) which originates on the dorsolateral surface of the opisthotic.

In pholidophorids, leptolepids and other primitive teleosts the subtemporal fossa presumably served principally for the origin of the adductor operculi and there is usually an anterior, less well-marked depression for the origin of the adductor hyomandibulae. The first recognizable depression which may be considered to be the homologue of the subtemporal fossa of pholidophorids and teleosts is found in fossil neopterygians (parasemionotids, *Heterolepidotes*, *Aspidorhynchus*, *Dapedium*, *Lepidotes* and *Pachycormus*; Patterson 1975: figs 97–9, 102, 106, 108, 112) although in *Amia* and *Lepisosteus* there is no obvious subtemporal fossa.

In *Perleidus* (Patterson 1975: fig. 115) and *Australosomus* (Nielsen 1949: figs 2, 29) there is a large subtemporal fossa, but this is presumed to be the homologue of both the anterior depression and subtemporal fossa of fossil halecomorphs, pholidophorids and teleosts.

In summary, the subtemporal fossa appears to be a specialization of later actinopterygians which in halecomorphs and teleosts serves for the origin of the adductor operculi.

In *Latimeria* (Millot & Anthony 1965: fig. 31) the dorsal hyoid constrictor has differentiated into an adductor hyomandibulae and an adductor operculi. The origin of the adductor hyomandibulae is remote from the adductor operculi and below the jugular canal; by comparison with selachians and chondrosteans this condition is presumed to be derived, as is the double articulation of the head of the hyomandibula. In the Devonian *Nesides* a distinct fossa (Bjerring 1977: fig. 22, ar.m.ad.hy) below the jugular canal must have served for the origin of the adductor hyomandibulae and a more dorsal fossa behind the dorsal hyomandibular articulation contained the adductor operculi. Identical fossae are recognizable in the rhipidistians *Ectosteorhachis* (Romer 1937: fig. 2) and *Rhizodopsis*. In *Eusthenopteron* (Jarvik 1954: fig. 21A, B; 1975: fig. 13A, B) the so-called 'process for the attachment of adductor muscles of hyomandibula' (Bjerring 1971: fig. 8) forms the posterior boundary of a depression which, by analogy with *Nesides* and *Latimeria*, also served for the origin of the adductor hyomandibulae.

There is no adductor hyomandibulae in Recent dipnoans and it is likely that the loss of this muscle is correlated with the reduction of the functional importance of the hyomandibula following fusion of the palate with the braincase.

10. *Origin of dorsal mandibular constrictor muscle.* The constrictor dorsalis is undifferentiated in living chondrosteans (Edgeworth 1935: 48), where it forms a large and powerful protractor hyomandibularis which originates dorsally on the postorbital process. A similar constrictor dorsalis is also characteristic of selachians where it has its origin on the postorbital process and extends downwards to insert on the inner (medial) surface of the palatoquadrate. In selachians it is called the levator maxillae.

In *Polypterus* the constrictor dorsalis has differentiated into four distinct muscles, the levator arcus palatini, protractor hyomandibularis, dilatator operculi and musculus spiracularis (Allis 1922: 254), but in all living neopterygians it differentiates into only two muscles (Lauder 1980),

the levator arcus palatini and the dilatator operculi, with the posterior portion of the levator arcus palatini inserting on the hyomandibula (= protractor hyomandibularis).

From this evidence it is clear that primitively in actinopterygians the posterior portion of the constrictor dorsalis (levator arcus palatini) was attached to the hyomandibula. The condition in living chondrosteans, where the anterior portion of the levator arcus palatini is missing, must be considered derived and related to the reduction of the palatoquadrate and its loss of contact with the braincase. In *Polypterus* the levator arcus palatini and protractor hyomandibularis originate together, the levator arcus palatini inserting on both the dorsal edge of the entopterygoid and the hyomandibula while the protractor hyomandibularis also inserts (via a membrane) on the dorsal edge of the palatoquadrate and the anterior edge of the hyomandibula. Both of these muscles, in being inserted to the suspensorium, may be equated with the single levator arcus palatini of neopterygians. The presence of separate levator arcus palatini and protractor hyomandibularis muscles in *Polypterus* is considered derived and related to the reduction of the posterodorsal corner of the palatoquadrate (otic process), which has allowed part of the levator arcus palatini to insert on the hyomandibula and then eventually to separate off as a distinct muscle. A separate protractor hyomandibularis is not seen in any other living fish (other than chondrosteans: see above) and it is doubtful that one existed in rhipidistians as postulated by Jarvik (1954: fig. 26).

There is no evidence of separate areas for the origins of dilatator operculi and levator arcus palatini muscles in any palaeoniscid and it is unlikely that these muscles differentiated. The constrictor dorsalis is postulated to have originated on the postorbital process, much as in *Polypterus* and selachians. With the elongation of the spiracular canal in more advanced actinopterygians a new area was made available for the hyoid constrictor, anterior to and above the hyomandibular facet. This area, first recognizable in *Perleidus* and parasemionotids, is termed the dilatator fossa. In lepisosteids, halecomorphs and pholidophorids the anterior area of the dilatator fossa housed the levator arcus palatini and the posterior area the dilatator operculi. In leptolepids (Patterson 1975: 387) the dilatator fossa only housed the dilatator operculi as in Recent teleosts, and is separated by a crest of bone from the area of origin of the levator arcus palatini.

In *Latimeria* (Millot & Anthony 1958) the dorsal constrictor has apparently differentiated into two muscles much as in neopterygians. The so-called 'levator arcus palatini' runs from in front of the dorsal hyomandibular facet to insert on the hind edge and inner (medial) surface of the palatoquadrate. The partial insertion of this muscle on the inner palatoquadrate surface is considered primitive for osteichthyans and gnathostomes, while the condition in actinopterygians, where the levator arcus palatini inserts on the outer surface of the palate, is derived. The effect this different origin has on elevation of the palate has been commented on elsewhere (Gardiner 1973: 121). It suffices to add that the action of the 'levator arcus palatini' in *Latimeria* merely pulls the palatoquadrate inwards and backwards. Anteriorly the 'levator arcus palatini' originates on the prootic behind the spiracle, not on the postorbital process as in selachians and actinopterygians. The dilatator (elevator) operculi in *Latimeria* is a small muscle lying just behind the 'levator arcus palatini' and which has presumably evolved in parallel with that in actinopterygians. It is difficult to see where the dorsal constrictor would have inserted in rhipidistians, but by comprison with actinistians, it must have originated behind the spiracular groove on the anterodorsal face of the lateral commissure. In *Eusthenopteron* (Jarvik 1954: fig. 23) the constrictor dorsalis could only have originated on the lateral commissure just anterior to the post-temporal fossa; in *Ectosteorhachis* (Romer 1937: figs 2, 6) and *Rhizodopsis* there is a well-marked depression in this area.

In dipnoans the constrictor dorsalis has not separated from the adductor mandibulae (cf. holocephalans) and this is considered a specialization related to autostyly (Miles 1977: 121).

11. *Endolymphatic duct.* In *Acipenser* the endolymphatic organ is club-shaped and extends into the cranial cavity, but in *Polypterus*, *Lepisosteus*, *Amia* and most teleosts it is shorter and confined to the otic capsule. In *Mimia* there is a gutter running from near the junction of the posterior semicircular canal with the sinus superior to the dorsal surface of the cranial cavity in

front of the dorsal fontanelle. This must have housed the blind-ending endolymphatic organ. In *Moythomasia*, on the other hand, the gutter for the endolymphatic duct opens into the posterior dorsal fontanelle and the duct was probably still open, as in chondrichthyans, placoderms and Devonian dipnoans. Unfortunately in one specimen of *Mimia* figured by Gardiner (1973: fig. 4, mcc) the area of the braincase around the end of the endolymphatic ducts had not completely ossified and this, together with the report of a median intramural chamber in *Dapedium* (Patterson 1975: 413), led Miles (1977: 102) to postulate the presence of a median supraotic cavity in actinopterygians. However, there is no such cavity in any living chondrichthyan, actinopterygian or *Latimeria* and it is better regarded as a specialization confined to some dipnoans, rhipidistians and tetrapods.

The endolymphatic duct is primitively open in gnathostomes and its closure in actinopterygians is considered a specialization. There is no evidence of a hypertrophied endolymphatic sac in actinopterygians.

Miles (1977: 103) has argued that the anterior division of the so-called supraotic cavity of primitive dipnoans is a synapomorphy shared with choanates. However, Young (1980: fig. 10) has described what he considers to be a posterior 'endolymphatic diverticulum' in the placoderm *Brindabellaspis* and states that this shows some resemblance to the supraotic cavity of Devonian dipnoans. But the supraotic cavity of rhipidistians and choanates is related to the endolymphatic duct which passes through it onto the roof of the neurocranium, and is primitively divided into a posterior median division and an anterior paired division. The 'endolymphatic diverticulum' of *Brindabellaspis* has none of these features and can in no way be homologized with the supraotic cavity.

12. *Pterosphenoid pedicel*. Patterson (1975: 409) proposed that this was a primitive actinopterygian feature, mainly because he recognized the relationship of this structure to the intramural chamber for the superficial ophthalmic nerves in *Kentuckia*, *Kansasiella* and caturids. From the condition in *Moythomasia* (see p. 230) it is now more certain that he was correct in homologizing the upper part of the pterosphenoid pedicel with that intramural chamber.

In *Moythomasia* (Fig. 29) the pedicel is often only partially developed, much as in *Pteronisculus magnus* (Nielsen 1942: 90) and Kansas palaeoniscid B (Watson 1925: 843), but in some specimens of *Moythomasia* (Fig. 30) it is complete and the lower portion is believed to have been formed by the prootic, as in *Macrepistius* (Schaeffer 1971: fig. 4). A similar pedicel is seen in *Amia* and its fossil relatives but here it is formed entirely by the pterosphenoid and meets the ascending process of the parasphenoid ventrally. In other caturids only the dorsal portion of the pedicel is present ('*Aspidorhynchus*', Patterson 1975: fig. 101) or sometimes only that part which envelops the superficial ophthalmic nerves (*Caturus*, *Heterolepidotus*, *Osteorachis*). In the larger pholidophorids (Patterson 1975: 409) the upper pterosphenoid portion is often present while in the Sinemurian *Leptolepis* only the lower prootic portion is developed. As in Recent teleosts, however, where the pedicel is frequently well developed, it consists mainly if not entirely of membrane bone.

From this we may conclude that the presence of a pterosphenoid pedicel is primitive, at least for actinopterygians, whereas enclosure of the superficial ophthalmic nerves in a separate bony canal is possibly a primitive osteichthyan feature (cf. *Youngolepis*).

13. *Prootic bridge and posterior myodome*. In vertebrate embryos the relationships of the orbital cartilage are surprisingly constant. Posteriorly it is invariably attached to the polar cartilage (or trabecula) by a pila antotica. The bases of the pilae antoticae are joined by a transverse connective cartilage, the acrochordal, which eventually forms the crista sellaris, dorsum sellae or prootic bridge.

In selachians (*Pristiurus*, Matveiev 1925: fig. 2; *Scyllium*, de Beer 1937: 69; *Squalus*, Holmgren 1940: 94; *Torpedo*, de Beer 1937: 69), dipnoans (*Neoceratodus*, Sewertzoff 1902: fig. 1) and amphibians (*Ambystoma*, Stöhr 1879) the orbital cartilage and pila antotica develop early, whereas in actinopterygians (*Polypterus*, Moy-Thomas 1934; *Acipenser*, Sewertzoff 1928;

Lepisosteus, Hammarberg 1937; *Amia*, Pehrson 1922; *Salmo*, de Beer 1927) these structures develop later and lag behind the auditory capsule, polar cartilage and trabecula. In selachians the dorsum sellae appears early, but in actinopterygians its development is considerably delayed, often until after the lateral walls of the braincase are completed. This delay in actinopterygians is often attributed to the development of the myodome, but the dorsum sellae is equally delayed in *Polypterus* and *Acipenser*, fishes without a myodome.

We now know that there are palaeoniscids without a posterior myodome (*Mimia*, *Moythomasia*) and that this was probably the primitive condition for actinopterygians (Gardiner 1973; Gardiner & Bartram 1977). We also know that the relationships of the profundus are quite varied (see above), but that bone in the position of the pila antotica always separates the trochlear, optic and oculomotor nerves from the trigeminal foramen. It is difficult then to concede that, because of the varying relationships of the profundus, the pila antotica is a secondary structure in *Polypterus*, *Acipenser*, and *Salmo* as de Beer (1937) and Schaeffer (1971: 6) assumed. It is even more difficult to accept its absence in *Lepisosteus* (de Beer 1937), where the difference is that the pila antotica lies somewhat more anteriorly than in other forms.

The dorsum sellae is assumed to have been ossified by the basisphenoid in *Mimia* (Gardiner & Bartram 1977: 230) and *Moythomasia*, as in *Polypterus*, but in all other actinopterygians it is formed by the prootics. The abducens nerve passes out below the dorsum sellae in *Mimia*, *Moythomasia* and *Polypterus*, behind it in *Acipenser*, in front and above in *Lepisosteus* (where the myodome is assumed to have been secondarily lost – see below), whereas in all other actinopterygians where a myodome is present the abducens pierces the prootic bridge.

An ossified prootic bridge (dorsum sellae) is also present in the anterior moiety of the braincase of actinistians and rhipidistians (Romer 1937, Thomson 1967, Schaeffer 1968) and is not missing as erroneously suggested by Gardiner (1973: 108). The lateral wall of the neurocranium of *Latimeria* is presumed to exhibit the primitive gnathostome condition, with the profundus, trochlear, optic and oculomotor nerves all passing through separate canals. The dorsum sellae is ossified by the basisphenoid and this bone also contains the foramina of the oculomotor and profundus nerves, as in *Polypterus*, whereas the abducens nerve leaves the braincase behind the dorsum sellae as in *Acipenser*.

In the rhipidistians *Ectosteorhachis* (Romer 1937: fig. 2) and *Eustherionopteron* (Jarvik 1954: fig. 1c) it may be inferred that the dorsum sellae, as in *Latimeria* and *Nesides*, is ossified by the basisphenoid and that the abducens nerve did not pass through it.

The dorsum sellae is cartilaginous in Recent dipnoans but ossified in the Devonian forms. In *Griphognathus* the profundus is supposed to pass out below and behind the dorsum sellae (Miles 1977: fig. 10), but this canal (V_1) could be more convincingly interpreted as transmitting the abducens nerve. In *Chirodipterus* the dorsum sellae lies further posteriorly than in *Griphognathus*, the profundus passed out above it, and the canal for the abducens (Miles 1977: figs 17, 35) is said possibly to originate between the facial and trigeminal canals, above the dorsum sellae.

In chondrichthyans such as *Heterodontus*, *Torpedo* and *Hydrolagus* the dorsum sellae is a stout bar of cartilage and the abducens nerve exits with the trigeminal above and slightly behind it. In *Squalus*, however, the abducens leaves through a separate canal below and posterior to the dorsum sellae (Jollie 1962: fig. 5.10).

In the placoderms *Buchanosteus* (Young 1979: figs 5, 6) and *Kujdanowiaspis* (Stensiö 1963b: fig. 26) the abducens has a separate canal which leaves the brain behind the root of the trigeminal, much as in *Squalus*.

I conclude that primitively in osteichthyans the dorsum sellae was ossified by the basisphenoid bone and in the primitive gnathostome the abducens nerve passed out below and behind it.

Posterior myodomes are not present in the primitive actinopterygian braincase (*Polypterus*, living chondrosteans) and are also absent in the Gogo palaeoniscids. There is little doubt that at least three of the rectus muscles originated on the basisphenoid pillar in *Mimia* and *Moythomasia* (Gardiner & Bartram 1977: 237), but whether or not the external rectus muscle originated here or in the back of the orbit ventrolateral to the abducens canal could not be determined, though it seems unlikely that it originated posteriorly. In *Polypterus* three of the

muscles (superior, inferior and external recti) arise from a short tendinous stalk with its origin on the basisphenoid immediately posterior to the optic foramen in a homologous position to those in selachians, while the fourth (internal rectus) takes origin anterior to the optic foramen. Similarly in *Acipenser* the four recti muscles attach to the cartilaginous interorbital region. The rectus muscles also originate on the basisphenoid in *Latimeria*, and a distinct pit in front of the basiptyergoid process in *Holoptychius* (Jarvik 1972: fig. 20B) and *Youngolepis* (Chang 1982: fig. 15B) must also have served for the origin of all four muscles. In *Acanthodes* (Miles 1973a: fig. 9; Jarvik 1977: fig. 3A) the perichondrally ossified basisphenoid pillar may have been related to these muscles. Primitively in gnathostomes the rectus muscles originated on the interorbital septum posterior to the optic nerve. In *Lepisosteus* the origins of all four rectus muscles have moved onto the basiptyergoid process (which is made up of the prootic; the basisphenoid is absent) and this is considered to be a specialization, as are the path of the abducens nerve and the loss of the myodome. In *Amia*, on the other hand, the superior, internal and inferior recti muscles originate on the transverse bolster of the basisphenoid and the external rectus enters the myodome. Myodomies only occur in more advanced actinopterygians (*Amia* and teleosts among living fishes), presumably as a result of the backward growth of the external rectus muscles onto that area of the basisphenoid immediately below and lateral to the pituitary.

In *Kentuckia* the myodome is represented by small paired depressions lateral to the pituitary vein foramen and ventral to the abducens canal. The ventral otic fissure lies more posteriorly than in *Mimia* or *Moythomasia* and I have argued elsewhere (Gardiner 1973: 106; Gardiner & Bartram 1977: fig. 8) that this is a consequence of the enlargement of the myodome (but see Schaeffer & Dalquest 1978); the larger the muscle canal is, the further back lies the fissure (see also Patterson 1975: 543). With this increase in size of the myodome the ventral otic fissure migrated further posteriorly until it became confluent with the vestibular fontanelles, and the enlarged dorsum sellae, which in *Mimia* and *Moythomasia* is ossified by the basisphenoid, is now ossified by the prootic. Consequently the ventral otic fissure is represented by the prootic/basioccipital suture, not the basisphenoid/basioccipital suture as in the Gogo palaeoniscids and *Polypterus*. Alternative explanations are provided by Schaeffer & Dalquest (1978) and Bjerring (1978).

14. *Anterior and middle cerebral veins.* Primitively, both these veins were well developed in actinopterygians, the anterior cerebral vein leaving the telencephalon recess high up through a transversely-directed canal in front of the epiphysial crest and trochlear nerve, whereas the middle cerebral vein left the cranial cavity through the metencephalic recess (*Mimia*, *Polypterus*) or the recess for the optic lobe (*Pteronisculus*, *Moythomasia*) but always behind the trochlear foramen.

Canals for the anterior and middle cerebral veins are present in *Mimia*, *Moythomasia*, *Kansasiella* (Poplin 1974: fig. 20, v, v.cer.ant), *Pteronisculus* (Nielsen 1942: fig. 6, v, v.cer.ant) and *Polypterus* (Allis 1922: 228), and in *Polypterus* both veins run into the supraorbital vein as in larval *Lepisosteus* (Hammarberg 1937: figs 25–27).

Despite the fact that the middle cerebral vein fails to develop in *Amia* (Bertmar 1965) and the anterior cerebral vein is absent in adult *Lepisosteus*, both veins were present in para-semionotids, *Caturus*, *Heterolepidotus*, '*Aspidorhynchus*', *Macrepistius*, *Dapedium*, *Lepidotes*, *Pachycormus*, pholidophorids and leptolepids (Patterson 1975: 412). Both veins occur in most living teleosts but according to Bertmar (1965: 122) and Patterson (1975: 411) have migrated to a more posterior position during the ontogeny and phylogeny of the group; the middle cerebral vein now falls into the jugular vein.

The position of the anterior cerebral vein in non-teleostean actinopterygians is remarkably constant but the same cannot be said for the middle cerebral vein. Primitively the canal for the middle cerebral vein originated in the optic recess above the trigeminal canal and behind the trochlear foramen. It passed down through the pterosphenoid to emerge in the orbit below and behind the pterosphenoid pedicel in the roof of the ganglion recess (for the gasserian and lateralis ganglia), close to the opening of the superficial ophthalmic canal. This is the condition seen in *Moythomasia* and most caturids; also in pholidophorids and leptolepids except that in

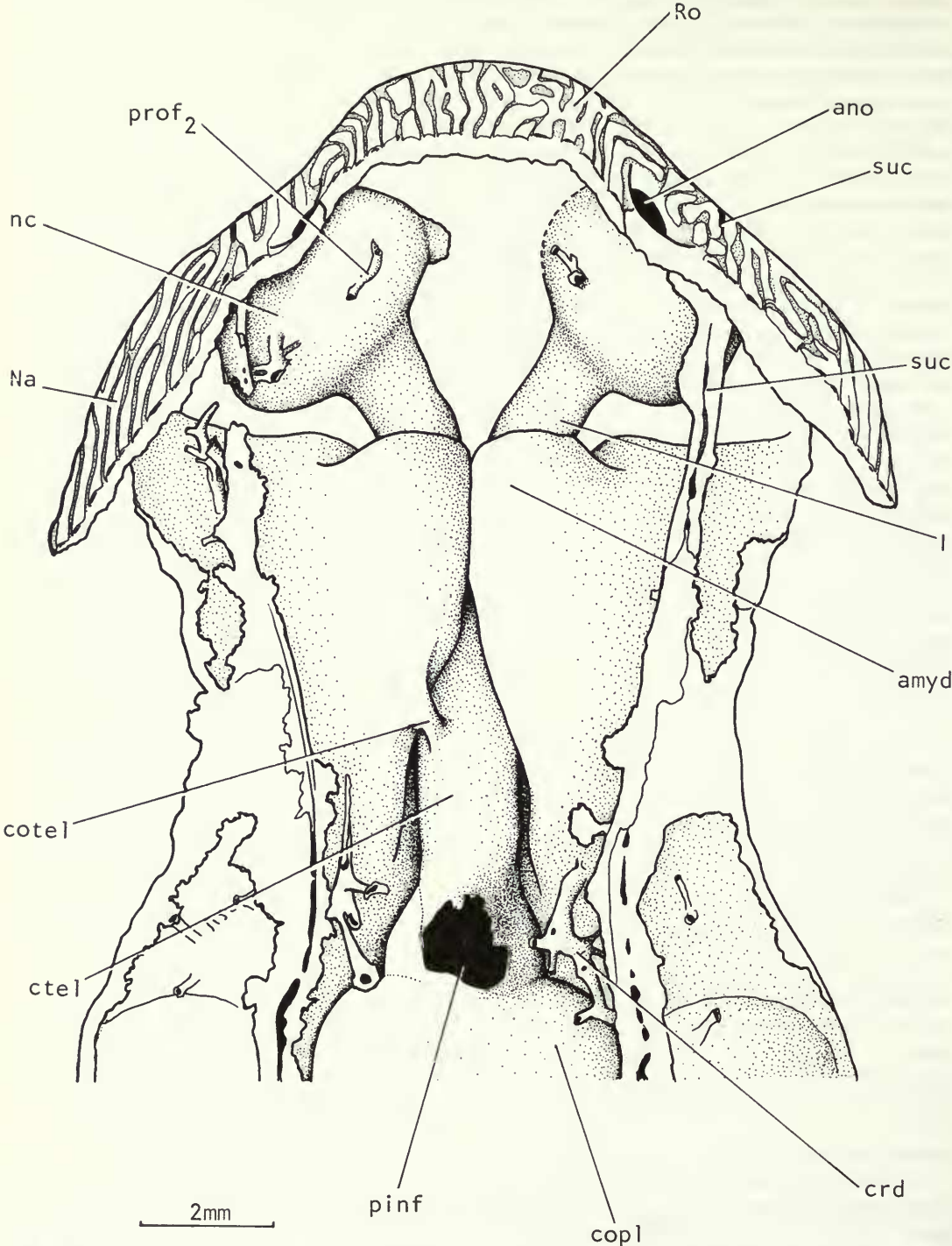


Fig. 33 *Mimia toombsi* Gardiner & Bartram. Preserved orbitotemporal and ethmoid parts of the neurocranium and attached dermal bones, in dorsal view, from BMNH P.56476.

the latter two groups the ophthalmic canal is missing and the foramen for the middle cerebral vein opens in line with the groove for the superficial ophthalmic nerves.

Thus primitively the trigeminal and middle cerebral vein canals lay close together (see particularly *Mimia*) and consequently it is not surprising to find the former capturing the latter in many teleosts.

In *Latimeria* the anterior cerebral vein leaves the cranial cavity through a separate foramen in the anterior wall of the orbit and falls into the supraorbital vein (Millot & Anthony 1958; Robineau 1975: 46) much as in *Polypterus*. There is, however, doubt as to whether or not a true middle cerebral vein occurs. Millot & Anthony (1958: fig. 5) indicated a middle cerebral vein passing behind the dorsal prefacial process of the prootic and running into the jugular vein immediately in front of the jugular canal, whereas Robineau (1975) said it was absent, adding that the ventrolateral sinus which lies in the posterior cranial cavity between the dura mater and cranial wall is its likely homologue. If a true middle cerebral vein is present in *Latimeria* then by comparison with actinopterygians it would pass out between the two parts of the cranium with the trigeminal nerve, as reported by Millot & Anthony (1958).

In *Neoceratodus* the anterior cerebral vein is much as in *Latimeria* and actinopterygians, passing through a separate foramen in the orbital wall and falling into the supraorbital vein (Spencer 1893: fig. 15). In the Devonian dipnoan *Griphognathus* Miles (1977: fig. 61) has demonstrated an extensive epiphysial plexus similar to that reported in *Latimeria* (Robineau 1975: 46) and in one specimen found a pair of foramina in the orbitotemporal for the exit of two branches of the anterior cerebral vein (cf. *Torpedo*, Holmgren 1940: fig. 154). In *Chirodipterus*, however, Miles (1977: figs 17, 47; see also Stensiö 1963b: fig. 43c) has also demonstrated the presence of a perichondrally-lined canal passing posterolaterally under the utricular recess and opening into the jugular canal, which undoubtedly housed the middle cerebral vein in life. Although other workers (*Chirodipterus*, Säve-Söderbergh 1952: fig. 6; *Dipnorhynchus*, Thomson & Campbell 1971: fig. 32) have restored the canal for the middle cerebral vein to a more dorsal position, all agree that it lies behind the facial and trigeminal canals. This must be a dipnoan specialization since primitively in osteichthyans the middle cerebral vein leaves the cranium in front of the trigeminal nerve or between the trigeminal and facial nerves (*Mimia*, *Ectosteorhachis*).

In rhipidistians a canal for the anterior cerebral vein has been described in *Rhizodopsis* (Säve-Söderbergh 1936), *Ectosteorhachis* (Romer 1937: fig. 8, unlabelled) and *Eusthenopteron* (Stensiö 1963b: fig. 50A). In *Ectosteorhachis* (Romer 1937: fig. 8) there was also an anastomosis between the anterior cerebral veins reminiscent of the epiphysial blood plexus of *Latimeria*, *Griphognathus* and the embryonic stages of actinopterygians and selachians. The path of the middle cerebral vein in *Ectosteorhachis* is represented by a large canal which lies below and between the trigeminal and facial canals and opens into the jugular trough. A narrower canal in a similar position has also been described in *Glyptolepis* (Jarvik 1972: fig. 21B). On the other hand in *Eusthenopteron* Bjerring (1971: fig. 17) has suggested that the middle cerebral vein passed dorsal to the trigeminal canal as in actinopterygians (see also Jarvik 1980: 186).

In selachians the anterior cerebral vein is as in osteichthyans whereas the middle cerebral vein, which in development passes in front of the root of the trigeminal nerve (Holmgren 1943: fig. 57, v.c.int; Bertmar 1965: fig. 9), passes through the trigeminal foramen with the trigeminal nerve in the adult and falls into the jugular vein (cf. teleosts).

15. *Sclerotic bones*. In *Mimia* the sclerotic ring may be comprised of two, three or four segments, or may be a complete ring. The only possible explanation for these varying conditions is to assume that there were always four ossification centres and that ontogenetic fusion occurred. Similarly in *Pteronisculus*, where there are normally four segments, three have been recorded in some instances (Nielsen 1942), and in *Moythomasia* there may be two segments (*M. durgaringa*) or four (*M. nitida*, Jessen 1968). The majority of palaeoniscids also have four segments (*Cheirolepis*, *Watsonichthys*, *Mesonichthys*, *Nematopychius*, *Amblypterus*, *Gonatodus*, *Cornuboniscus*, *Paramblypterus*, *Commentrya*, *Birgeria*). There are also four sclerotics in *Australosomus*, *Lawnia*, *Chondrosteus*, *Acipenser*, *Dorypterus*, *Bobasatrania* and some

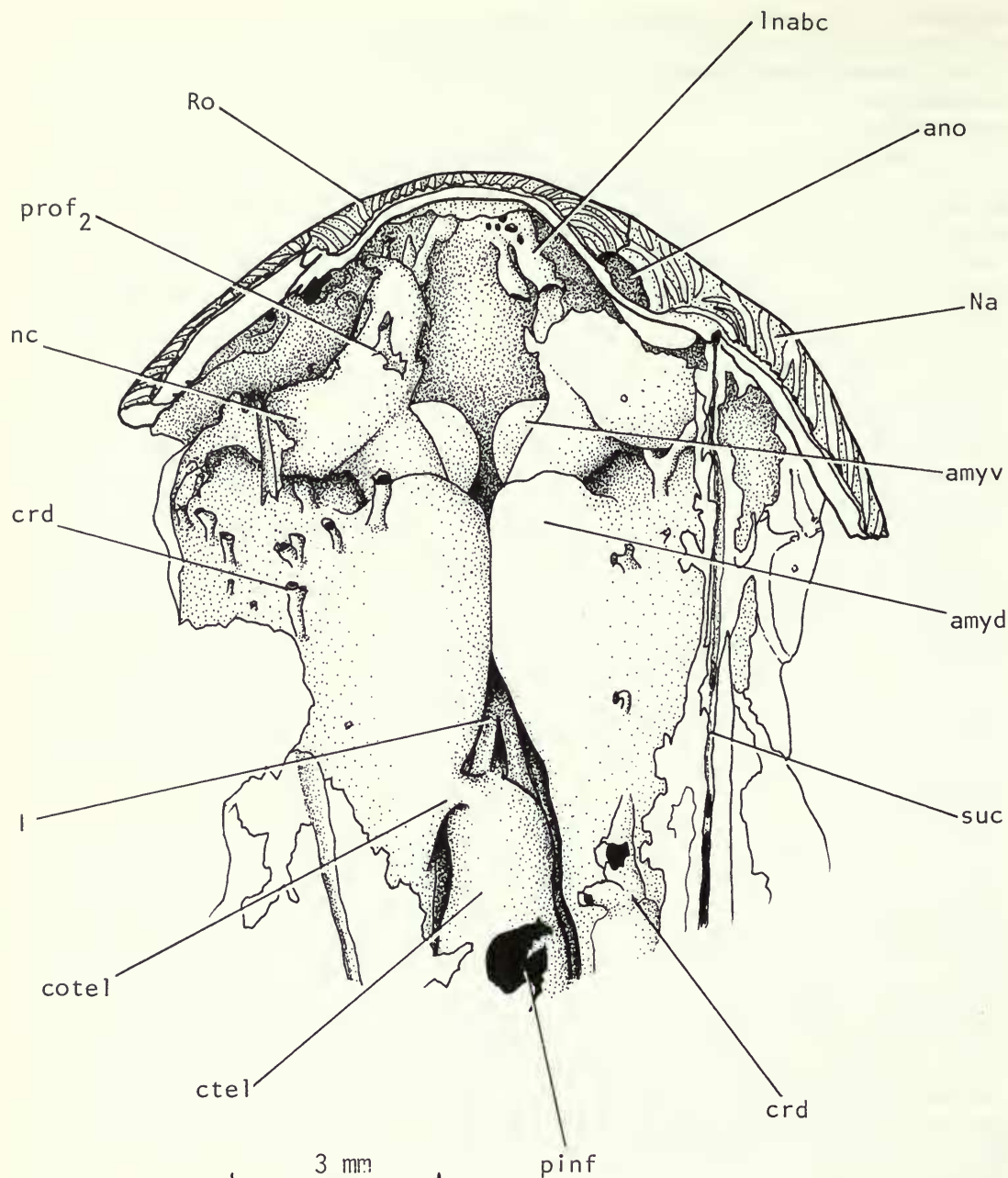


Fig. 34 *Mimia toombsi* Gardiner & Bartram. Preserved ethmoid region of the neurocranium and attached dermal bones, in dorsal view, from BMNH P.56505.

pholidophorids, but in *Pholidophorus macrocephalus*, leptolepids and other teleosts there are only two (Patterson 1975: 414). There are similarly two segments in fossil actinopterygians such as *Lepidotes* and *Dapedium* (Edinger 1929) and in *Aspidorhynchus*, *Pachycormus*, *Mesturus* and *Macromesodon*. From this evidence we may conclude that a sclerotic ring composed of four segments is primitive for actinopterygians.

Elsewhere within the osteichthyans the number of segments is much greater. Thus in

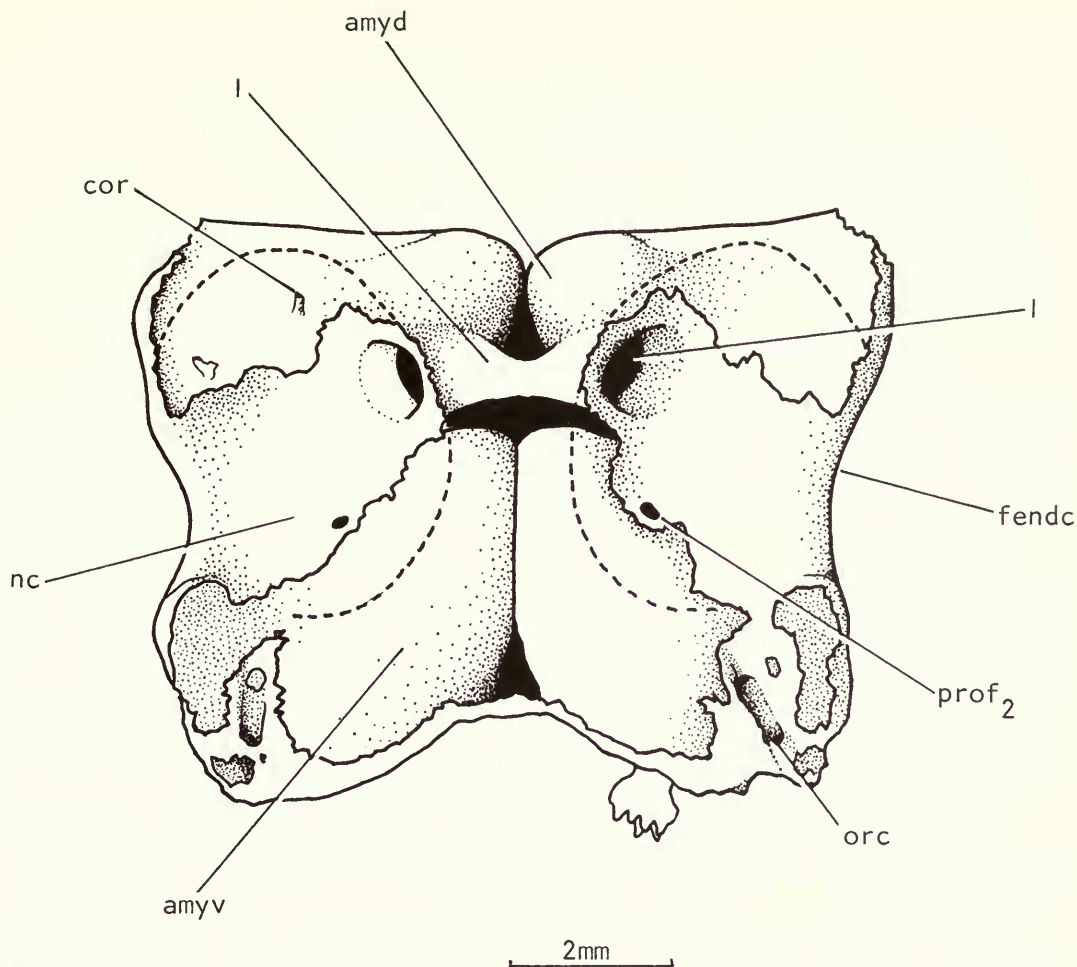


Fig. 35 *Mimia toombsi* Gardiner & Bartram. Ethmoid region in anterior view, from BMNH P.53240. Broken lines denote limits of nasal capsules.

actinistians there are 18 to 20 in *Latimeria* (Millot & Anthony 1965). There are approximately 18 in the onychodont *Strunius* (Jessen 1966), 17 in the rhipidistian *Osteolepis*, and in *Eusthenopteron* as many as 35 segments (Jarvik 1944a). Within the dipnoans similar large numbers have been recorded in *Rhinodipterus* and *Dipterus* (more than 20 in each; Schultz 1970), but in the Devonian *Griphognathus* Miles (1977: 249) has described a single undivided ring. Miles decided this was 'a specialized feature brought about by the late ontogenetic fusion of numerous segments'.

Elsewhere in gnathostomes a sclerotic ring occurs in placoderms and acanthodians. In the latter group it always appears to comprise five segments (*Acanthodes*, *Protogonacanthus*, *Homalacanthus*, *Triazeugacanthus*, Miles 1965, 1966; *Cheiracanthus*, *Mesacanthus*, Watson 1937) but in placoderms the number is usually four (*Phlyctaenaspis*, *Arctolepis* Heintz 1962: 36; *Coccosteus*, *Holonema* Miles 1971b: 141). Only three have been recorded in *Bothriolepis* (Stensiö 1948) but in the rhenanids *Gemuendina* and *Jagorina* there are as many as 10 and 12 segments respectively (Stensiö 1950). In *Goodradigbeeon* (White 1978: 196) there is a circlet of four dermal plates but a further dermal plate articulates with part of the inner margin of this ring and an almost complete layer of perichondral bone covered both surfaces of the calcified sclerotic cartilage (see BMNH P.33734, P.50455). Although the so-called sclerotic ossifications

recorded in the agnathans *Jamoytius* and *Lasanius* (Ritchie 1968: 21) appear to be no more than the remains of the pigmented retina, and in other anaspids are probably circumorbital scutes (Janvier 1981: 137), distinct sclerotic bones occur in a number of celphalaspids (Janvier 1981) and both dermal and perichondral elements can be recognized in specimens of *Atelaspis* (*Aceraspis*) *robusta* (BMNH P.2138) and *Hemicyclaspis* (BMNH P.8809, P.8801). These apparently number four segments.

A sclerotic ring is thus a synapomorphy of advanced 'agnathans' and gnathostomes and which in gnathostomes and cephalaspids primitively consisted of four segments.

A sclerotic ring of more than 12 segments is a synapomorphy of osteolepids, actinistians, onychodonts, porolepids and choanates.

Ethmoid region and associated dermal bones

The ethmoid region is well preserved in *Mimia* and the cartilage was entirely enclosed in a thin layer of perichondral bone. Such a layer also lines the cavities of the nasal capsules and the many canals. There was no endochondral ossification in the ethmoid region. The perichondral bone is closely applied to the overlying dermal bones except in the region beneath the premaxillae and the anterior part of the rostral.

Mimia toombsi

The orbital face of the postnasal wall is shown in Fig. 36; it is divided sagittally by the very thin interorbital septum. This septum widens in the dorsal region where the paired, diverging perichondrally-lined canals of the olfactory nerves pass into the ethmoid region. There is an elongated dorsolateral gap in the ossification of this canal (gI, Figs 13, 36), as in *Boreosomus* (Nielsen 1942: fig. 62).

Above and below the olfactory nerves are pairs of depressions in the postnasal wall. The lower pair (amyv, Figs 13, 36, 40) have a greater rostral extent than the upper pair (amyd, Figs 13, 36, 40). A similar set of depressions is present in *Boreosomus* (Nielsen 1942: fig. 65) and *Pteronisculus* (Nielsen 1942: fig. 17). These depressions must be anterior myodomes as Nielsen suggested, the dorsal pair for the superior oblique muscles and the ventral pair for the inferior oblique muscles.

The wall separating the dorsal myodomes in *Mimia* is pierced by a few minute holes. Much larger apertures are found in a corresponding position in other primitive actinopterygians. Thus in *Boreosomus* (Nielsen 1942: fig. 62) there is a large fenestra connecting each pair of myodomes. In *Saurichthys* (Stensiö 1925: fig. 10B), where the anterior myodomes are very shallow, there are fenestrae in a similar position to those of *Boreosomus*, and the interorbital septum dividing the single anterior myodome of *Australosomus* (Nielsen 1949: fig. 2) is also pierced by a large fenestra.

Another conspicuous feature of the postnasal wall is a pair of marked lateral notches slightly below the level of the olfactory nerve canals. Such notches occur in *Pteronisculus* and *Kansasiella*, and mark the lateral limits of the fenestra endonarina communis, described below.

The paired articulation for the palatoquadrate cartilage faces posterolaterally at the junction of the postnasal wall and suborbital shelf.

The anterodorsal corner of the orbit and the postnasal wall are pierced by a large number of pores, many more than have been recorded in other primitive osteichthyans, and they form three groups. The first consists of canals leading from the anterodorsal corner of the orbit and dorsolateral parts of the dorsal anterior myodomes to the skull roof (nasals), the second of canals leading from the upper part of the postnasal wall to the cavity of the nasal capsule, and the third of canals leading from the lower part of the postnasal wall to the nasal cavity, to the premaxillae and rostral bones and to the nasobasal canals (see below).

The canals of the first group are of variable calibre and occur medial and lateral to the supraorbital sensory canal (crd, Figs 34, 36; cor, Figs 35, 36, 40). There are at least nine such canals on the left side and fewer on the right in BMNH P.56505, an acid-prepared specimen on which most of the following description is based. The most posterior of these canals leads to the

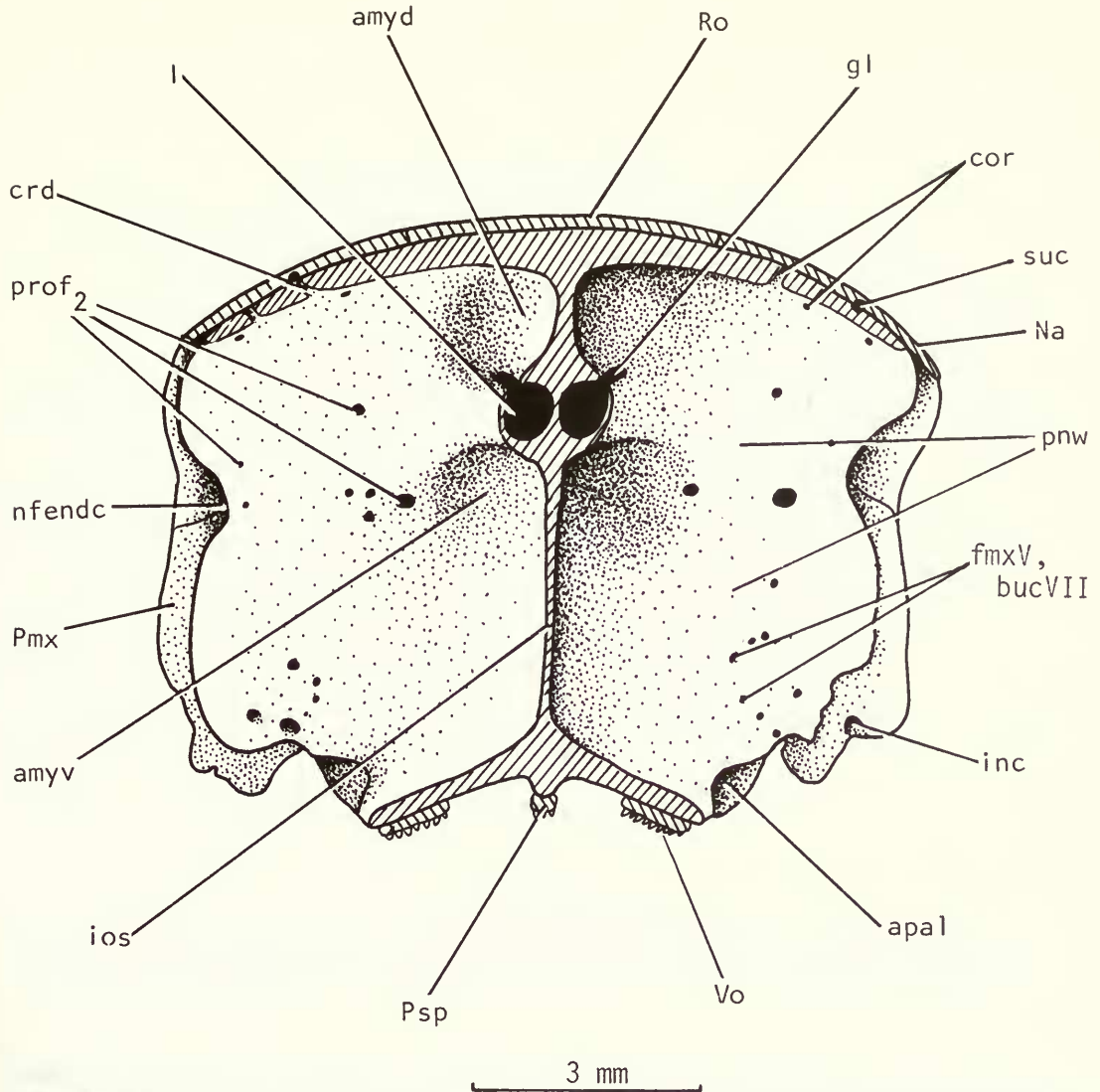


Fig. 36 *Mimia toombsi* Gardiner & Bartram. Braincase and associated dermal bones as if cut transversely through anterior region of orbit, to show the postnasal wall in posterior view; cut surfaces cross-hatched. From BMNH P.56505.

supraorbital sensory canal. This sensory canal lay in an open groove, bounded by raised walls, beneath the nasal bone. The raised walls fitted in turn into a groove, lined with perichondral bone, on the dorsal surface of the neurocranium. The canal connected with this groove and presumably conveyed branches of the superficial ophthalmic nerve. The remaining canals presumably carried other branches of the superficial ophthalmic nerves to the skull roof.

The canals of the second group are also asymmetrical in number in BMNH P.56505. On the left side one canal passes through into the posterior wall of the nasal capsule. Below this are four canals which pass slightly dorsally into the posteroventral corner of the cavity. Finally, two fine canals pass into the nasal capsule close to the lateral notch in the postnasal wall. On the right side the dorsal canal is symmetrical in position to that on the left side, but there is only one lateral canal and two ventral canals. Of the last two the lateral canal is the largest in the group. These orbitonasal canals are assumed to have carried branches of the profundus nerve.

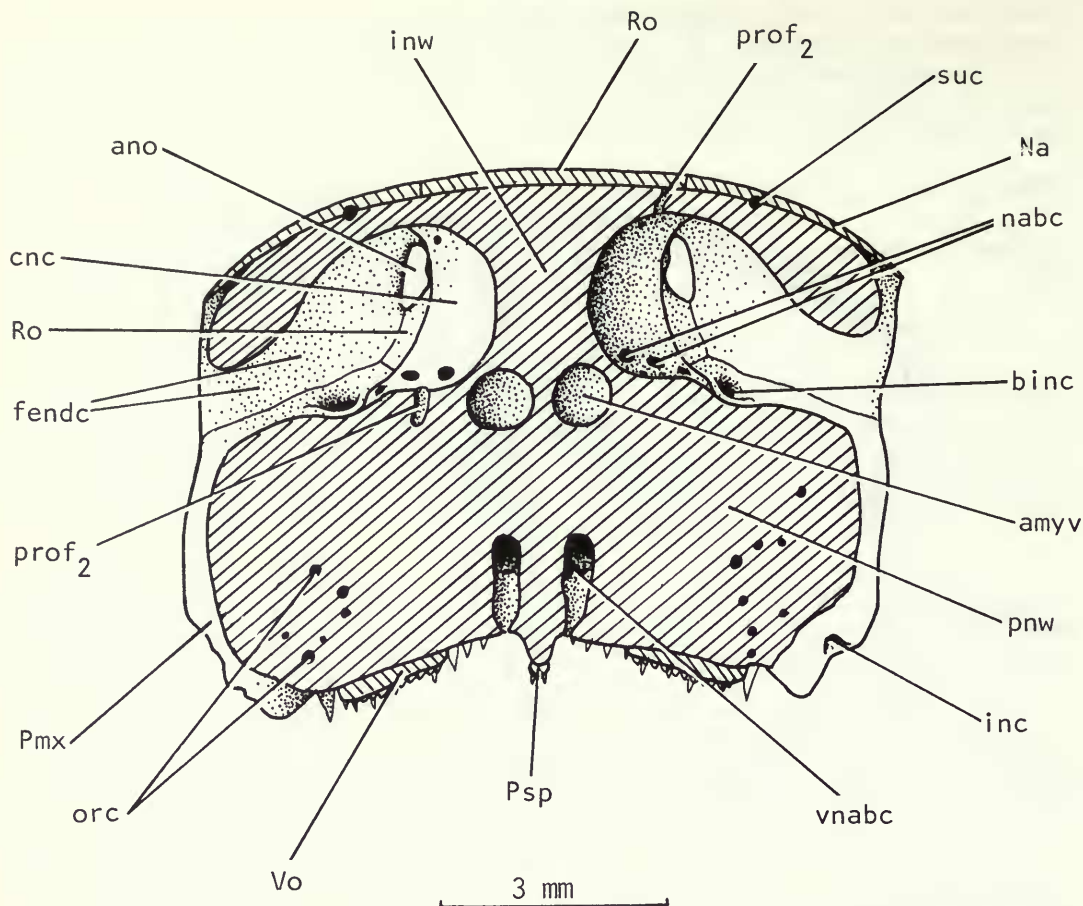


Fig. 37 *Mimia toombsi* Gardiner & Bartram. Braincase and associated dermal bones as if cut transversely through the nasal capsules, and viewed from the rear, from BMNH P.56505. Cut surfaces cross-hatched.

The pores of the ventral group are also asymmetrical in distribution, and in the directions which their corresponding canals take. Although these canals are visible for most of their length, their exact anterior limit and their minute terminal branches are not always clear. To investigate them more fully would involve further damage to the specimen: the specimen which was serially sectioned was deficient in this region. On the right side is an arc of six pores and two pores respectively dorsal and lateral to these. The lowermost pore of the arc passes anteromedially into a groove on the neurocranium running in the same direction, just above the tooth row of the premaxilla. Canals from the three following dorsal pores in the arc run into this groove, which appears to end near the tip of the rostral bone. The groove is remote from the more lateral infraorbital sensory canal in the premaxilla, but nerve endings could have crossed the gap between the neurocranium and the dermal bone. The next pore in the series leads to a dorsally-directed canal which connects with the central of the three anterior nasobasal canals described below. This canal sends fine branches to the infraorbital sensory canal. The canal associated with the most dorsal pore of the arc is short and leads into the same sensory canal. The pore dorsal to the group just described leads to a dorsally-directed canal which anastomoses with the lateral anterior nasobasal canal. Finally, the lateral pore forms a short canal leading to the infraorbital sensory canal.

On the left side is an arc of five pores and one lateral to these. The lowermost leads to a canal

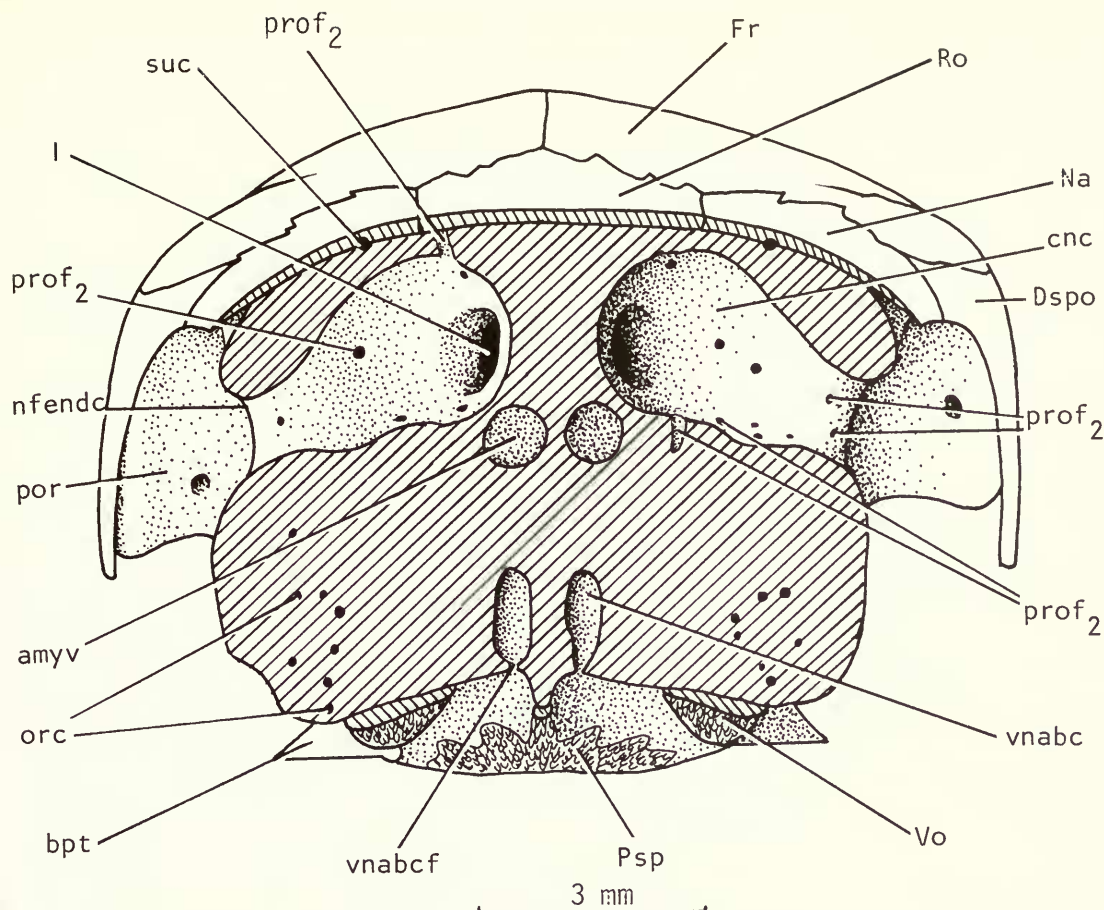


Fig. 38 *Mimia toombsi* Gardiner & Bartram. Braincase and associated dermal bones as if cut transversely through the nasal capsules, and viewed from the front, from BMNH P.56505. Cut surfaces cross-hatched.

and groove corresponding to that described on the right side. The next dorsal canal appears to turn into this groove while the third canal in the series runs parallel to the second and also joins the groove, after giving off a branch which anastomoses with the fourth canal. The fourth canal joins the most posterior of the three left side ventral nasobasal canals. The most dorsal pore of the left side arc leads to a highly-branched canal; two of these branches go to the rostral area, and two pass dorsally to open into the floor of the nasal capsule. At several points along this canal there are short branches to the infraorbital sensory canal. Finally, the pore lateral to the arc also leads to the sensory canal. The complicated system of canals described above is not found in any living fish but by comparison with living and fossil dipnoans it may be suggested that they transmitted either maxillary branches of the trigeminal or buccal branches of the facial nerve, or in some cases both.

The bulbous nasal capsules are more completely enclosed in bone than in other actinopterygians. The walls enclosed the ventral, posterior and the medial half of the anterior surface of the capsule, leaving a large fenestra endonarina communis. The latter faces antero-laterally and slightly dorsally, and is covered, except for the fenestra exonarina anterior, by the nasal and narrow strips of the rostral and premaxillary bones. The posterior nasal tube opened laterally between the nasal and the notch in the postorbital wall. The canal for the olfactory nerve opened into the posteromedial wall of the nasal cavity.

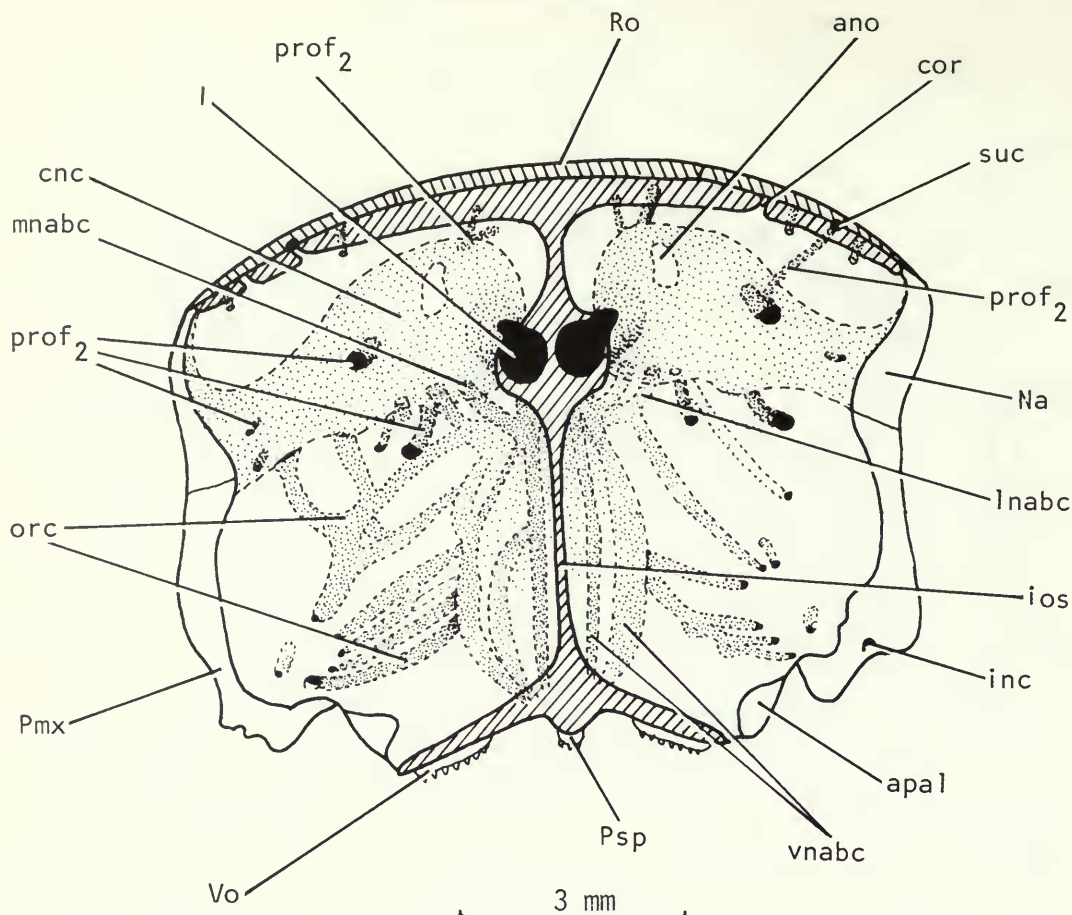


Fig. 39 *Mimia toombsi* Gardiner & Bartram. Braincase and associated dermal bones as if cut transversely through anterior region of orbit; showing postnasal wall in posterior view. Cut surfaces cross-hatched. The intramural canals and cavities lined with perichondral bone are stippled. From BMNH P.56505.

Apart from the pores piercing the posterior wall and floor of the nasal capsule there are two other groups of pores. On the left side two canals, the posterior one branched, run from the roof of the cavity to the rostral above. On the right side there is only one such canal. These canals ($prof_2$, Figs 37, 38, 40) presumably contained twigs of the upper profundus branch which crossed the rear wall of the nasal cavity, as in *Griphognathus* (Miles 1977: fig. 63) and *Porolepis* (Jarvik 1942: fig. 42).

The pores of the second group are larger and pierce the anteroventral corner of the nasal cavity in a row of three (nabc, Fig. 37; mnabc, lnabc, Figs 39, 40), medial to the opening of the dorsal branch of the infraorbital sensory canal (binc, Fig. 37) in the premaxilla. They lead to pores opening beneath the rostral (but not piercing it) and appear to be homologous to the two nasobasal canals (in a similar position) in *Eusthenopteron* (Jarvik 1942: 470). Communicating with the anterior ends of the medial and lateral nasobasal canals in *Mimia* is a further set of canals (three on the left, two on the right) which pass posteroventrally to open by a pair of pores in the roof of the mouth, one on either side of the midline (vnabcf, Figs 38, 41). These are the homologues of the ventral nasobasal canals of *Eusthenopteron* (Jarvik 1942: 470) and presumably transmitted branches of the palatine nerve.

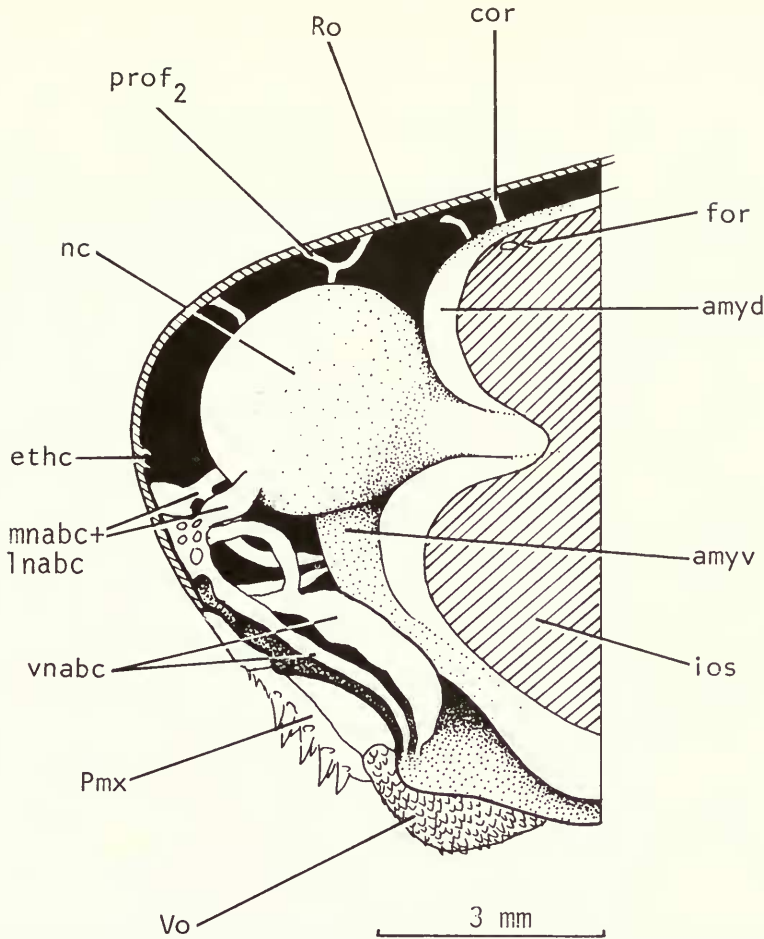


Fig. 40 *Mimia toombsi* Gardiner & Bartram. Ethmoid region of braincase and associated dermal bones in sagittal section, from BMNH P.56505; showing perichondrally lined canals. Sectioned bone cross-hatched.

The ethmoid region of the neurocranium is covered dorsally and anteriorly by a median rostral and paired nasals and premaxillae.

The rostral extends a little over 25% of the length of the skull roof (Figs 41, 101). The rostral is bounded posteriorly by the frontals, which it joins in a serrated suture. The lateral edges of the bone are straight, forming sutures with the nasals except where these two bones are emarginated to form the anterior nostril. At the level of the anterior nostril, the rostral curves sharply ventrally (Fig. 40) and less sharply laterally, thus forming a rounded protruding tip to the snout. The anteroventral edge of the rostral is V-shaped, forming sinuous sutures with the dorsomedial edges of the premaxillae (Fig. 41), which exclude the rostral from the border of the mouth. The external surface of the rostral bears the usual vermiculate pattern of ganoine ridges. The centre of radiation of the bone appears to occur slightly anterior to the mid-point of the line joining the anterior nostrils, at the point of greatest curvature of the bone. The ganoine ridges which extend posteriorly from this point to the frontals are long and parallel (Fig. 42). Anteriorly, the ganoine ridges form an irregular, maze-like radiation. The passage of the ethmoidal commissure is indicated on the external surface of the rostral by an arc of pores (four in BMNH P.56483), which extends through the centre of radiation to points on the lateral part of the suture between

the rostral and premaxillae. Internally this sensory canal lay in an open groove limited by two raised ridges of bone (Fig. 42).

The nasals are paired, narrow elongated bones flanking the rostral, and slightly shorter than this bone. The lateral border of the nasal forms a gentle, regular curve limiting the anterodorsal edge of the orbit; this border is not emarginated by the posterior nostril, as it is in many other palaeoniscids. Posteriorly, the nasal forms an oblique suture with the frontal and dermosphenotic. The anterior suture with the premaxilla is transverse and slightly curved. The external surface of the nasal bears long ridges of ganoine orientated along the length of the bone (Fig. 43). These are particularly narrow and closely-spaced near the orbital edge. The ganoine rugae become shorter anteriorly, close to the anterior nostril. The supraorbital sensory canal occupied a groove on the inner surface of the nasal for the first half of its course, but anteriorly was enclosed in a raised tube of bone which ends blindly at the level of the anterior nostril. The passage of the canal is indicated externally by a row of fine pores (five in BMNH P.56483). In many specimens (e.g. BMNH P.56483) the nasal bears a short pit-line anterior to, and in line with, the supraorbital canal; this pit-line probably represents the anterior continuation of the sensory canal, as in *Polypterus*.

The paired premaxillae are flat bones facing anteriorly and slightly laterally and ventrally, and form the anterior edge of the mouth. This edge bears two kinds of teeth. The larger kind forms a row of about ten inner teeth. These are deciduous, leaving large circular scars on the bone; they do not differentiate a sharply-defined enamel (acrodin) cap and match the major teeth on the dentary and maxilla. The smaller teeth, whose equivalents are also found on the last two bones, are exterior to the major teeth, and occur close to the edge of the mouth (Fig. 44). The lateral edge of the premaxillary tooth row gives way to a small area of overlap for the first infraorbital bone (lachrymal). The infraorbital sensory canal entered this area of the premaxilla. The lateral edge of the premaxilla lies alongside the lateral edge of the postnasal wall of the ethmoid region of the braincase below the posterior nostril; the edge of the premaxilla completes, with the nasal and dermosphenotic, the curve of the dorsal and anterior edge of the orbit. The two premaxillae form a short, straight median suture with each other. The sutures with the rostral and nasal bones are described above.

The ornament of the premaxilla is complex. Along the orbital edge it consists of the usual straight, narrow, parallel rugae and along the oral edge, close to the teeth, it is in the form of ganoine tubercles. Between these two regions extends an area of irregular, vermiculate rugae orientated mainly towards the tip of the snout. The pattern of sensory canal pores is also complex. An irregular line of pores passes from the ventrolateral corner of the bone to the suture with the rostral. This line belongs to the anterior part of the infraorbital sensory canal. Internally this canal was housed in a tube which becomes an open groove in the upper part of the bone (Fig. 44); the tube is pierced by fine pores which transmitted nerves from the buccal and maxillary rami of the facial and trigeminal nerves. A short, dorsal branch of the infraorbital sensory canal, enclosed in bone, opens internally into the nasal cavity before reaching the dorsal edge of the premaxilla. Apart from the pores belonging to the infraorbital sensory canal, there are others which vary in position and distribution from specimen to specimen. Thus in the right premaxilla of BMNH P.56505 these pores are distributed above and below the middle region of the infraorbital canal. The left premaxilla of the same individual has only the ventral pores.

The ethmoid region is partly covered ventrally by an anterior projection of the parasphenoid and by a pair of vomers (Vo, Figs 41, 50, 55). The vomers are small, triangular-shaped ossifications which lie medial to the articular facets for the palatoquadrates and in front of the postnasal wall. A median tongue of the parasphenoid passes between them (Psp, Fig. 50). The vomers are covered by sharply-pointed teeth, larger than those on the parasphenoid.

Moythomasia durgaringa

Unfortunately, no specimen of this species has been found so far in which the ethmoid region is well preserved. Nevertheless the orbital face of the postnasal wall is visible in several specimens. It is very similar to that described in *Mimia*; there is the same dorsolateral gap in the canals for the olfactory nerves (Fig. 7) and there are two anterior myodomes with the lower pair having the

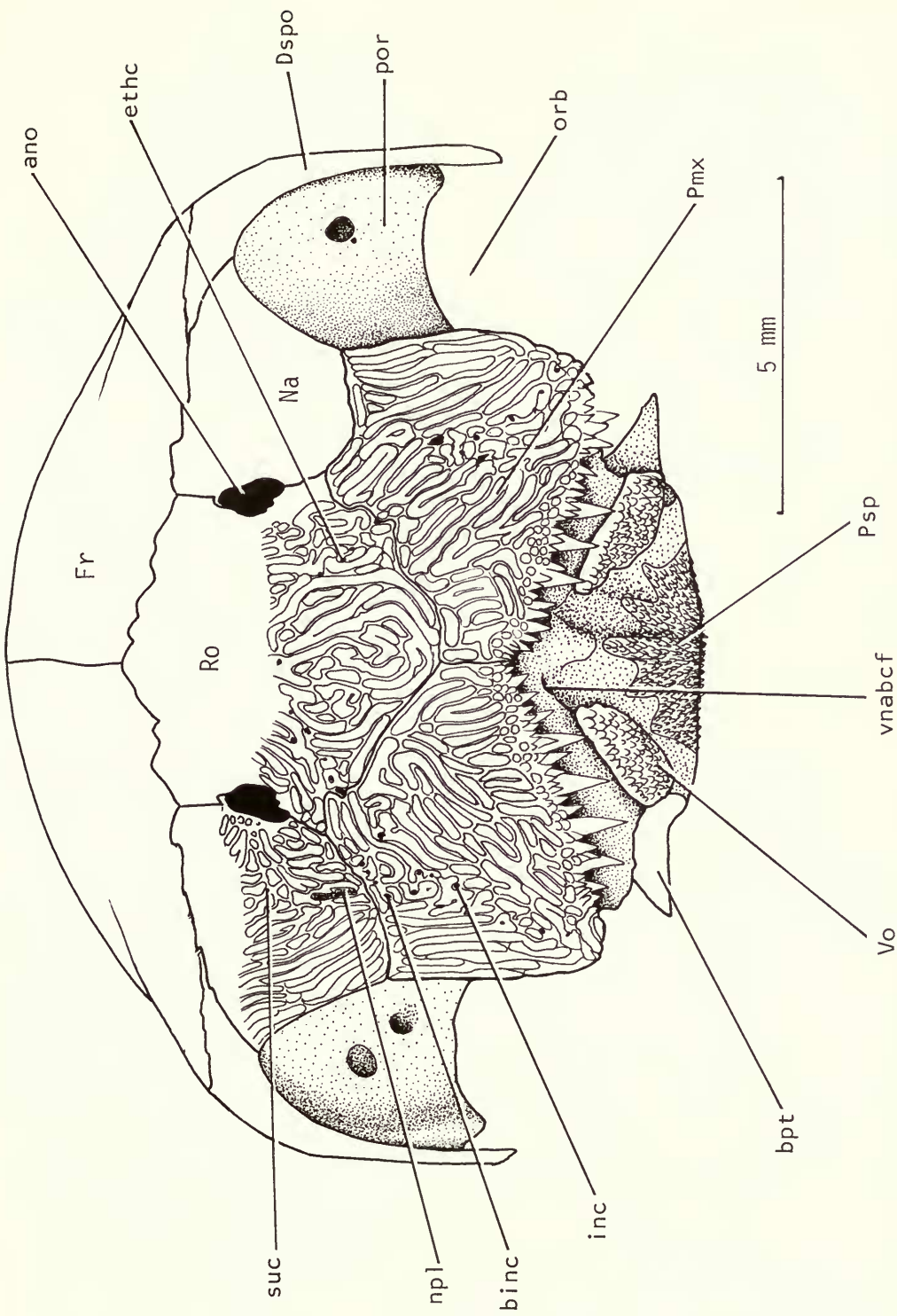


Fig. 41 *Mimia toombsi* Gardiner & Bartram. Braincase and associated dermal bones in anterior view, based on BMNH P.56505. Ornamentation only partly shown.

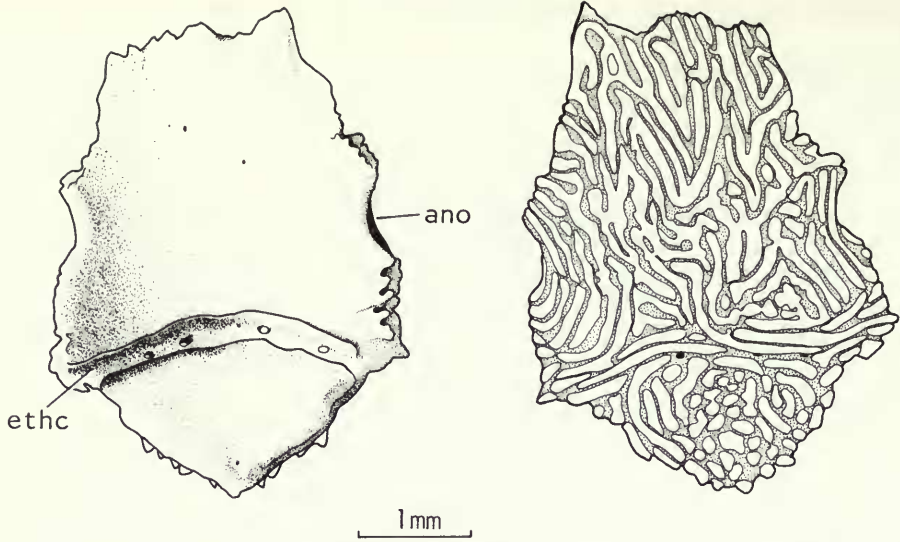


Fig. 42 *Mimia toombsi* Gardiner & Bartram. Rostral in posterior (left) and anterior views, from BMNH P.56483.

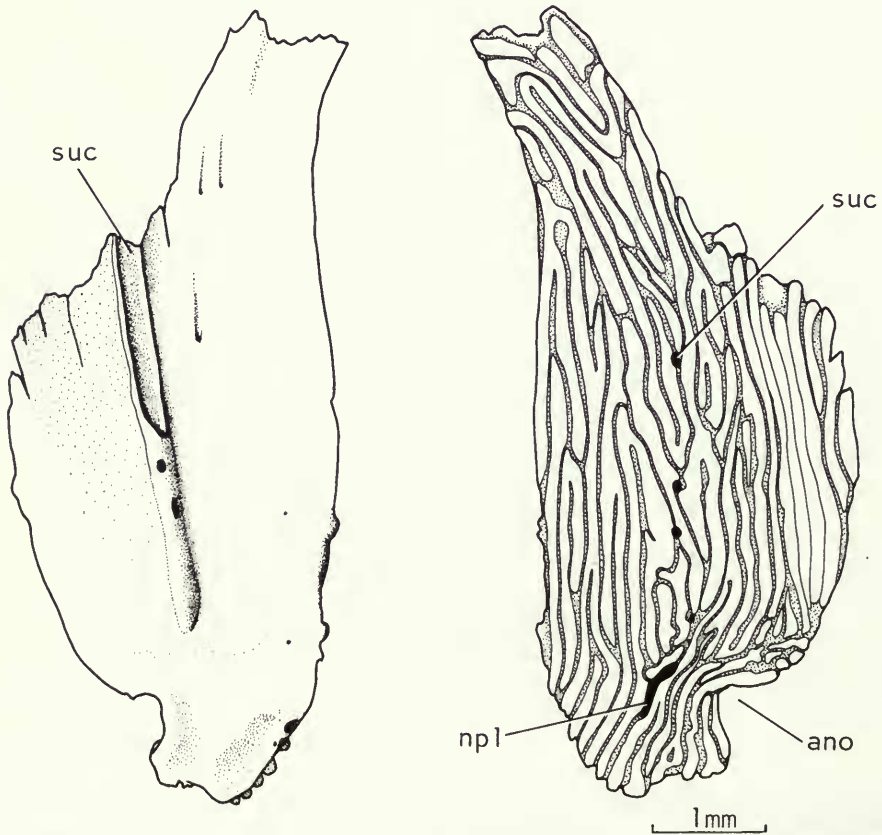


Fig. 43 *Mimia toombsi* Gardiner & Bartram. Right nasal in lateral (right) and medial views, from BMNH P.56483.

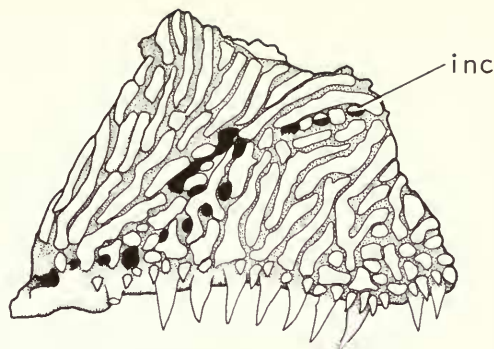
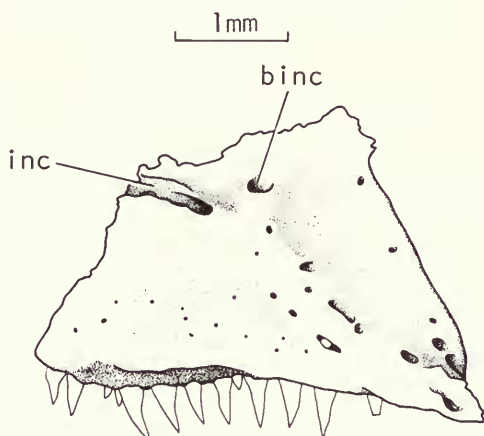


Fig. 44 *Mimia toombsi* Gardiner & Bartram.
Right premaxilla in lateral (above) and medial
views, from BMNH P.56483.



greater rostral extension. Similarly the articulations for the palatoquadrates occur at the junction of the postnasal wall and suborbital shelf, and the postnasal wall is pierced by a large number of pores. The nasal capsules are bulbous and are enclosed to the same extent as in *Mimia*.

The same dermal bones cover the ethmoid region as in *Mimia*, but their shape and extent are quite different. The rostral extends for over 25% of the length of the skull roof and forms a highly digitate suture with the frontals posteriorly. Behind the anterior nostrils the lateral edges of the rostral are straight and parallel, but at the level of the anterior nostrils, where the bone curves sharply ventrally, the lateral edges flare outwards and then converge, so that the anteroventral edge of the rostral is V-shaped (Figs 45, 48). Unlike *Mimia*, the rostral in *Moythomasia* separates the two premaxillae and takes part in the border of the mouth. The ornamentation of the rostral consists of very stout tubercles and ridges of ganoine, which for the most part have fused into an irregular maze-like configuration. The centre of radiation is considerably anterior to the anterior nostrils and the ethmoid commissural sensory canal passed through it. Internally this canal was housed in a tube, pierced by two fine pores (Fig. 45) which presumably transmitted branches of the buccal and maxillary nerves. On the ventral margin of the bone the ganoine tubercles are pointed and give way to one (Fig. 48) or two (Fig. 45) teeth which correspond to the smaller teeth on the premaxillae, maxillae and dentaries, external to the major, replaceable teeth.

The nasals are paired, narrow bones and the sutures between them and the rostral are straight except where they are interrupted by the notch for the anterior nostril. The lateral border of the nasal is emarginated by a much larger notch for the posterior nostril. Posteriorly, the nasal forms an oblique suture with the frontal and dermosphenotic, and ventrally it overlaps the premaxilla for a short distance (Fig. 48). Anteroventrally, a little beyond the notch for the anterior nostril,

the nasal loses contact with the rostral altogether and a large foramen is formed between the rostral, nasal and premaxilla. The external surface of the nasal bears massive fused tubercles and ridges of ganoine which laterally, near the orbital edge, are orientated along the length of the bone. The supraorbital sensory canal extended in a groove on the inner surface of the nasal and terminated at the level of the dorsal margin of the anterior nostril. The passage of the canal is indicated externally by a row of eight pores in BMNH P.53255 (Fig. 46). Lateral to and parallel with this sensory canal is an elongate foramen (p, Fig. 48). In other specimens (Fig. 46) this foramen is the same size as the sensory canal pores.

The flat, stout premaxillae face anterolaterally, and ventrally bear two kinds of teeth. There are never more than four of the deciduous larger kind, which have sharply-defined enamel caps (acrodin). The smaller, pointed teeth form an external row of some 15–20 (Fig. 48). Anteriorly the premaxilla is in sutural contact with the rostral but dorsally the suture gives way to a small area of overlap for the nasal. Posteriorly, above the tooth row, the posterior margin has a more extensive overlap area for the first infraorbital (lachrymal). The lateral edge of the premaxilla lies alongside the lateral edge of the postnasal wall and forms the lower margin to the posterior nostril.

The ornamentation on the premaxilla is similar to that on the rostral, with stout striae of ganoine dorsally and rounded tubercles ventrally. Internally the infraorbital sensory canal was housed for the most part in an open gutter, though the dorsal branch which opens short of the dorsal edge of the premaxilla was enclosed in a tube. The course of the infraorbital sensory canal is marked externally by a line of up to twelve pores which in some specimens are in the form of slits. Below the middle region of the infraorbital canal is a further series of four pores, which lead into a short canal within the bone. Internally this canal is pierced by three pores (p, Fig. 47).

The paired vomers are covered by sharply-pointed teeth, the posterior row of which is much enlarged (Gardiner & Bartram 1977: fig. 7). The vomers are widely separated, irregular in outline and lie medial to the articulation facets for the palatoquadrates (Fig. 7).

Ethmoid region: discussion

1. *Anterior myodome*. Two pairs of anterior myodomes appear to be present in most palaeoniscids (*Mimia*, *Moythomasia*, *Kentuckia*, *Pteronisculus*, *Boreosomus*). In the palaeoniscid *Kansasiella* (Poplin 1974: fig. 18), however, the ventral anterior myodome is median. In the pholidopleurid *Australosomus* there is a single, large paired anterior myodome ventral

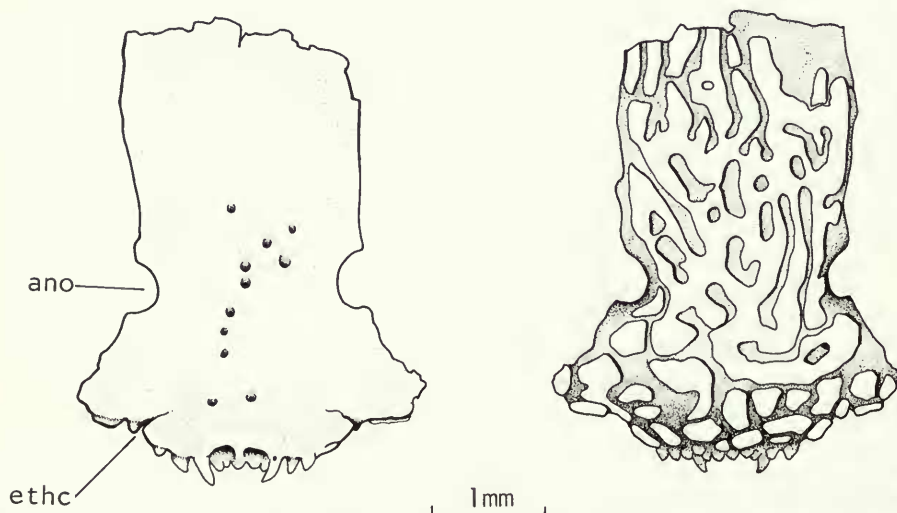


Fig. 45 *Moythomasia durgaringa* Gardiner & Bartram. Rostral in posterior (left) and anterior views, from BMNH P.53255.

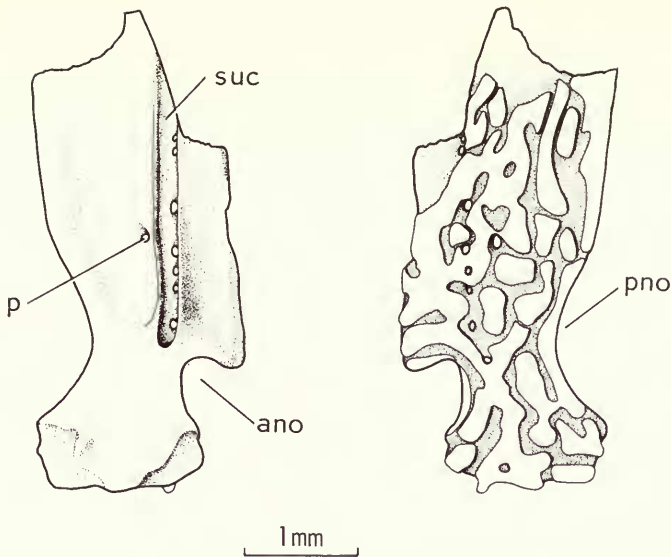


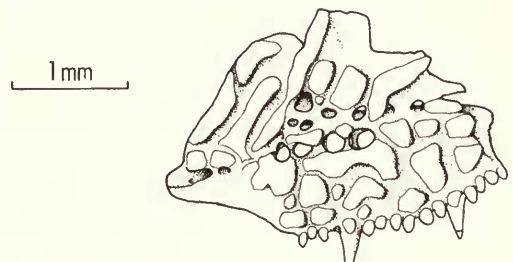
Fig. 46 *Moythomasia durgaringa* Gardiner & Bartram. Left nasal in lateral (right) and medial views, from BMNH P.53255.

to the olfactory nerve canal (Nielsen 1949: fig. 13). Two pairs of rather shallower anterior myodomes are present in *Saurichthys*, parasemionotids, *Macrepistus* (Schaeffer 1971: fig. 6) and *Dapedium*, and as in palaeoniscids the upper pair lie dorsal to the olfactory nerve canal and often communicate with one another through an interorbital fenestra. In some caturids (*Caturus*, *Heterolepidotus*, '*Aspidorhynchus*'), however, the dorsal myodome is obscured by an enlarged interorbital fenestra (Patterson 1975: fig. 102). In *Amia* both oblique muscles, together with a vein, pass through a large orbitonasal canal into the olfactory nerve canal and are attached to its floor.

In *Pachycormus* (Patterson 1975: 516) there is no ventral anterior myodome, and in this it resembles pholidophorids and Recent teleosts where there is a median, dorsal anterior



Fig. 47 *Moythomasia durgaringa* Gardiner & Bartram. Right premaxilla in medial (above) and lateral views, from BMNH P.53255.



myodome and where both pairs of oblique muscles enter the foramen olfactorium evehens; this is a specialization.

There is no anterior myodome in living chondrosteans or *Lepisosteus*; the oblique muscles originate separately in the former but together in the latter. In *Polypterus* the two muscles are separated as in chondrosteans and dipnoans, but the superior oblique muscle enters the funnel-like opening of the profundus canal where it attaches to the medial wall.

In *Nesides* and *Euporosteus* (Jarvik 1942: fig. 75A, B) there is said to be a single small myodome ventral to the olfactory nerve, similar to that in *Australosomus*, except that through it also ran the orbitonasal artery. In *Diplocercides* (specimen figured by Stensiö, 1922: pl. 3, fig. 1) there are two pairs of shallow ventral myodomes, and these depressions are in a position homologous to the origins of the superior and inferior oblique muscles in *Latimeria*, although in *Latimeria* myodomes are absent. The condition in dipnoans is less easy to interpret, but in larval *Neoceratodus* the superior oblique muscle originates in the upper anteromedial corner of the orbit, whereas the inferior oblique arises near the bottom corner. In adult *Neoceratodus* there are no anterior myodomes and Miles (1977) also failed to find any such structures in the Gogo dipnoans.

In the rhipidistian *Eusthenopteron* (Jarvik 1942: figs 49, 50, fo.m.obl), very shallow paired ventral pits have been described in the postnasal wall, which according to Jarvik (1942: 437) were probably the place of origin of the oblique muscles. No such depressions have so far been described in any other rhipidistian (*Ectosteorhachis*, *Rhizodopsis*, *Porolepis*, *Holoptychius*, *Youngolepis*); in *Glyptolepis* sp. (BMNH P.47838), however, there are two pairs of shallow ventral myodomes below the profundus canal, in a position homologous to the paired depressions in *Diplocercides*. No myodomes have been described in chondrichthyans but depressions have been noted in the perichondral lining of the front of the orbit in certain placoderms (*Brindabellaspis*, Young 1980: fig. 10), which presumably served as points of origin for individual muscles. A corresponding anteroventral depression in the floor of the orbit of *Macropetalichthys* (Stensiö 1963b: fig. 32) has been attributed to the inferior oblique muscle.

From this evidence we may conclude that anterior myodomes, like posterior myodomes, were primitively absent in gnathostomes and osteichthyans. Anterior myodomes have been independently acquired in actinopterygians, actinistians and some rhipidistians. In actinopterygians the anterior myodome typically consists of two pairs of shallow depressions, one pair above and the other below the olfactory nerve canal, whereas in actinistians and rhipidistians the two pairs of depressions are both below the olfactory nerve canal, in the floor of the postnasal wall.

2. Postnasal wall and nasal capsule. The ethmoid region of *Mimia toombsi* is traversed by a greater number of canals than in any other osteichthyan and the number of pores piercing the postnasal wall is correspondingly high. The dorsal group of canals (4–7) in the postnasal wall are presumed to have served for branches of the profundus nerve.

The ventral group of canals (5–8) pierce the ventrolateral corner of the postnasal wall (orc, Figs 37–40). The most lateral of these canals communicates with the infraorbital sensory canal and thus must have transmitted the buccal branch of the facial nerve. It is impossible to decide whether the remainder of these canals transmitted maxillary or buccal nerve branches or both. Several of these dorsal and ventral canals (orc, Fig. 39) communicate with the nasobasal canals (mnabc, lnabc, Fig. 39), which run from the nasal cavity to the rostral area and there communicate with a set of ventral nasobasal canals (vnabc, Figs 39, 40). Similar nasobasal canals are found in the floor and anterior wall of the nasal capsule of *Eusthenopteron* (Jarvik 1942: fig. 57), *Glyptolepis* (Jarvik 1972), *Youngolepis* (Chang 1982: fig. 14) and *Griphognathus* (Miles 1977: fig. 62(a), prog.V, V₂) and must be presumed to be a primitive feature of osteichthyans. In *Eusthenopteron* and *Glyptolepis* Jarvik (1942, 1972) considered that these nasobasal canals transmitted branches of the profundus nerve and that the palatonasal canal of *Eusthenopteron* served for a branch of the maxillary nerve. Rosen *et al.* (1981: 192), however, considered that the nasobasal canals in *Eusthenopteron* transmitted the truncus infraorbitalis and accompanying vessels. Miles (1977: 130) decided that in *Griphognathus* the dorsomedial of

the two nasobasal canals carried a ventral division of the profundus nerve, whereas the lateral canal transmitted the maxillary nerve.

Thus we may conclude that the nasobasal canals transmitted maxillary and buccal nerve branches as well as branches of the profundus nerve.

The olfactory organ in fishes is a blind sac, with a single anterolateral or ventrolateral aperture. This aperture is varyingly subdivided by flaps or more extensive tissue barriers into incurrent and excurrent openings. Each olfactory organ is surrounded by cartilage or bone apart from a single anterolateral aperture which serves for both incurrent and excurrent streams. This nasal capsule is developed in continuity with the front end of the trabeculae; a median septum nasi separates the right from the left capsule, the floor of the capsule is termed the solum nasi and the roof the tectum. This is essentially the condition in *Chlamydoselachus* and *Polypterus*.

Primitively in osteichthyans the postnasal wall is ossified by the lateral ethmoids (*Polypterus*, *Latimeria*, *Acipenser*, *Amia* and teleosts), but the only living fishes with any endoskeletal ossification anterior to the postnasal wall are *Amia*, teleosts and *Latimeria*. However, the nasal capsule is more or less completely perichondrally ossified in *Mimia*, *Moythomasia* and *Europorosteus* (Jarvik 1942: 556) and in *Eusthenopteron* (Jarvik 1972: fig. 66D) and *Griphognathus* there is also some endochondral bone present. In *Mimia* and *Moythomasia* the ethmoid region is a shell of thin perichondral bone with all the canals for nerves and blood vessels also surrounded by tubes of perichondral bone. Consequently it is difficult to recognize individual ossification centres in this region. Nevertheless, it would appear that paired lateral ethmoids were primitively developed in the postnasal wall of osteichthyans because paired lateral ethmoids are found in *Polypterus*, *Acipenser*, *Birgeria*, *Perleidus*, *Lepidotes*, *Caturus*, *Macrepistius*, *Amia*, pachycormids, Recent teleosts, *Macropoma* and *Latimeria* (Patterson 1975: 499).

In *Amia*, pholidophorids, *Hypsocormus* and Recent teleosts there are additional endoskeletal ossifications. Paired pre-ethmoids occur in *Amia* and *Hypsocormus*, a median supraethmoid, ventral ethmoid and anterior myodome bones are found in pholidophorids and up to five ossifications are present in some teleosts, including a median supraethmoid, ventral ethmoid and anterior myodome bones and paired capsular ethmoid bones. As Patterson (1975: 502) concluded, there is good evidence that the region anterior to the lateral ethmoids is a new formation in advanced actinopterygians. In other words there has been an increase in the number of ossification centres. From this I conclude that the primitive osteichthyan possessed one pair of ossifications in the ethmoid region, the lateral ethmoids, and that each olfactory organ was completely surrounded by bone apart from a lateral aperture.

3. *Dermal bones of the snout.* Primitively the roof of the nasal capsule in actinopterygians is covered by a broad, shield-like rostral, bordered by the frontals behind and the nasals laterally. The rostral contains a portion of the ethmoid commissure. This is essentially the condition in *Polypterus* and palaeoniscids. In most previous descriptions of palaeoniscids (e.g. Aldinger 1937; Moy-Thomas & Dyne 1938; Nielsen 1942, 1949; Gardiner 1963, 1967; Jessen 1968) the rostral is mistakenly called the postrostral, but it is now clear that it is penetrated by the ethmoid commissure in almost all instances. Re-examination of *Cheirolepis* (Fig. 49) has convinced me that the rostral is a single ossification (e.g. BMNH P.60533, P.4051a; GSM 88873; RSM 1973.12.150) and there is little evidence for considering it to be comprised of several ossifications as Gardiner (1963) and Pearson & Westoll (1979) have suggested. The evidence for a lateral postrostral in *Cheirolepis canadensis* (Pearson & Westoll 1979: fig. 3d, h) rests on the interpretation of a single specimen (BMNH P.6815). In my estimation this lateral postrostral is more reasonably interpreted as the rostral.

A similar shield-like rostral is also met with in pholidophorids (Patterson 1975: 497), perleidids, redfieldiids, ptycholepidids and *Dapedium*, but in *Pachycormus* (Patterson 1975: 511) the large median rostral has fused with the underlying, toothed, lateral dermethmoids. In parasemionotids (Patterson 1975: fig. 137), caturids (*Caturus*, *Furo*, *Heterolepidotus*, *Osteorachis*), amiids, many semionotids (*Acentrophorus*, *Lepidotes*) and *Lepisosteus* (Patterson 1975: figs 135, 136) the median rostral is reduced to little more than a tube around the

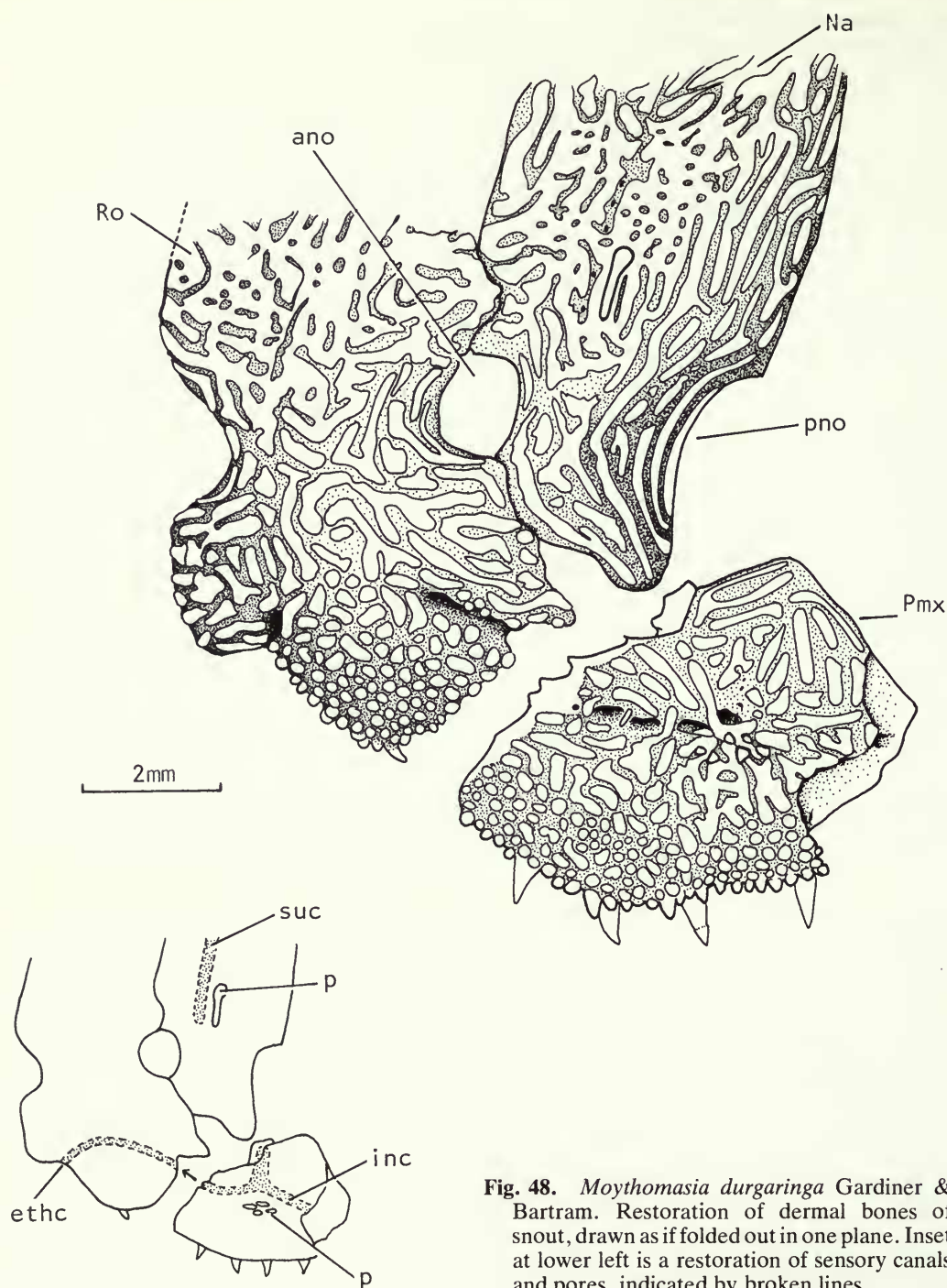


Fig. 48. *Moythomasia durgaringa* Gardiner & Bartram. Restoration of dermal bones of snout, drawn as if folded out in one plane. Inset at lower left is a restoration of sensory canals and pores, indicated by broken lines.

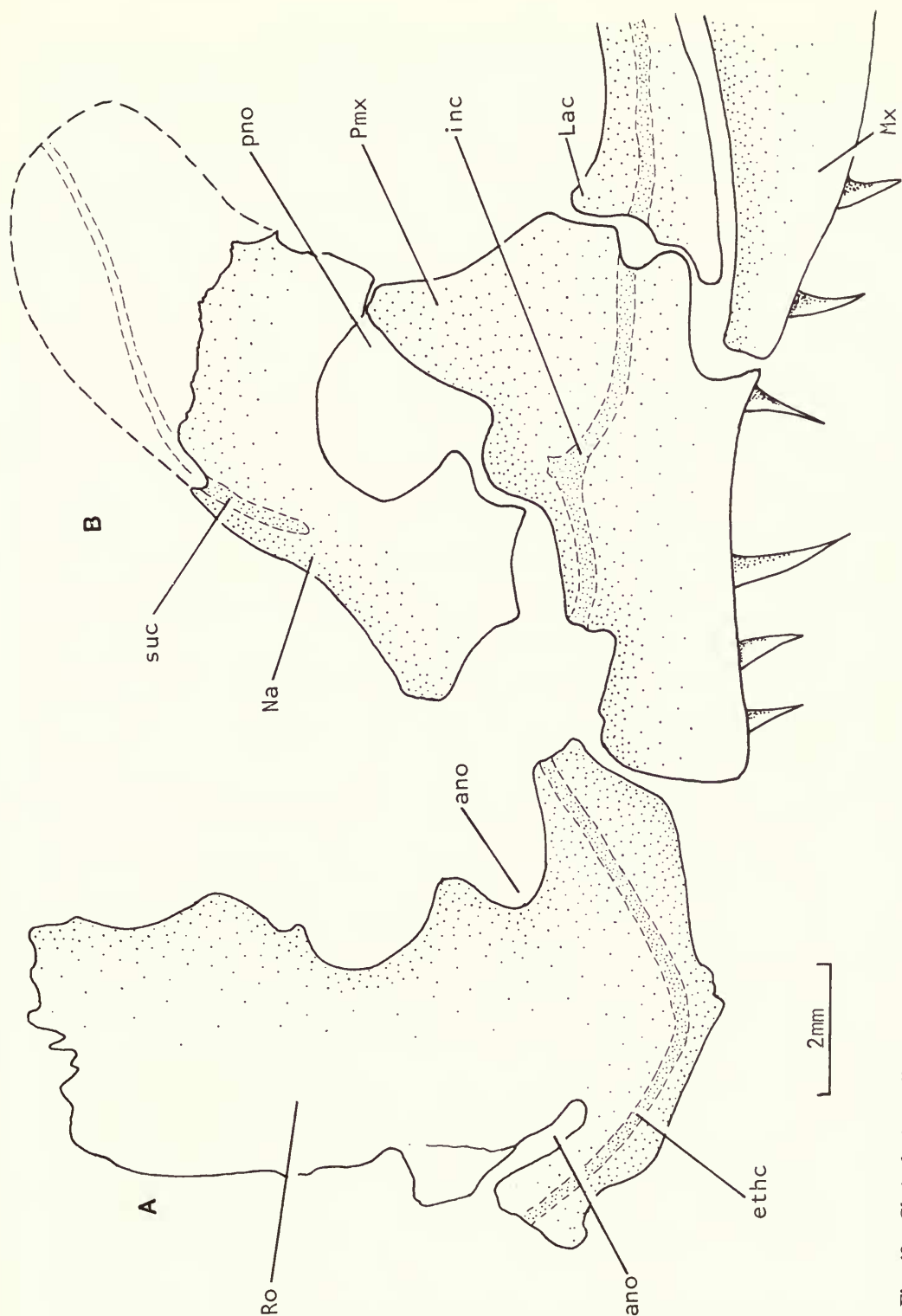


Fig. 49 *Cheirolepis trailli* Agassiz. Sketch restoration of dermal bones of snout in medial view. (A), rostral, from P.60553; (B), nasal, premaxilla, lachrymal and maxilla from P.53903a.

ethmoid commissure with the nasals meeting in the mid-line behind it. In teleosts, where the ethmoid commissure remains bone-enclosed (e.g. leptolepids, *Megalops*, *Elops*), the tube-like rostral is fused with the underlying dermethmoid as in *Pachycormus* (Patterson 1975: 511).

A median rostral is also found in *Holoptychius* (Jarvik 1972: figs 35, 36) where it is so small that it only just embraces the ethmoid commissure. The rostral of actinopterygians may have captured the middle part of the ethmoid commissure as Patterson (1975: 512) suggests, or conversely it may have been primitively associated with it. Support for the latter point of view is afforded by its presence in the rostrals of actinopterygians and *Holoptychius*, and for the former by the condition in actinistians, where in fossil forms (*Laugia*, *Rhabdoderma*, *Macropoma*) the ethmoid commissure is contained within the premaxillae as in some rhipidistians (*Eusthenopteron* Jarvik 1942; *Osteolepis* Jarvik 1948; *Megalichthys* Thomson 1964). In *Latimeria* the commissure is separate from the underlying premaxillae and bears four short bones along its length. An ethmoid commissure wholly contained within the premaxilla is found in early actinistians and osteolepiforms, and this is believed to be primitive. Conversely a shield-like rostral is considered synapomorphous for actinopterygians.

The remaining portion of the snout was primitively covered in actinopterygians by the paired, toothed premaxillae which contain the characteristic triradiate anterior portion of the infraorbital sensory canal and the greater part of the ethmoid commissure. The premaxilla in early actinopterygians has often been termed the rostro-premaxillo-antorbital because the premaxilla and antorbital of higher actinopterygians are believed to result from its subdivision (Gardiner 1963). However, it is better to regard this bone in early actinopterygians as the premaxilla as it is homologous with that bone in rhipidistians where it also bears replacement teeth and the triradiate portion of the infraorbital sensory canal.

A canal-bearing premaxilla is found in all Devonian palaeoniscids, ptycholepid and *Polypterus*, but in perleidids, parasemionotids, caturids, amiids, semionotids, pachycormids, pholidophorids and Recent teleosts the premaxillary and antorbital (canal-bearing) components are separate.

The nasal is single in actinopterygians with the exception of *Polyodon* and *Polypterus* where there are three. The nasal in *Cheirolepis* (BMNH P.65527, P.65528, P.4050) is very similar in shape to that of *Mimia* and there is little evidence to suppose it is composed of more than one ossification.

Tetrapods, like most actinopterygians, have a single pair of nasals, but elsewhere in osteichthyans the number is higher. In primitive actinistians (*Diplocercides* Stensiö 1937) there are five pairs of nasals, and some dipnoans (*Soederberghia* Lehman 1959) have as many as eight. In osteolepids, *Eusthenopteron* (Jarvik 1948: fig. 16) has three, *Megalichthys* and *Osteolepis* six, while the porolepid *Holoptychius* (Jarvik 1972: figs 35, 36) usually has five nasals. Primitively in osteichthyans there were probably four or more nasals. In primitive actinopterygians there was one.

In a previous publication (Gardiner 1963) I assumed that the antorbital branch of the infraorbital sensory canal primitively anastomosed with the terminal portion of the supraorbital canal between the nostrils in actinopterygians (see however Jollie 1969). The supraorbital canal does anastomose with the infraorbital canal in *Lepisosteus*, *Amia*, *Latimeria*, porolepids and osteolepids, but in dipnoans, *Cheirolepis*, *Mimia*, *Moythomasia*, *Polypterus*, chondrosteans and teleosts (Nybelin 1967) it does not.

The primitive osteichthyan condition probably lacks such an anastomosis. In the primitive actinopterygian the supraorbital canal passed between the nostrils as in chondrosteans, *Polypterus*, *Lepisosteus* and *Amia*. In *Latimeria* the supraorbital canal joins the infraorbital both in front of and between the nostrils, whereas in osteolepids and porolepids the supraorbital and infraorbital canals anastomose in front of the nostrils. In chondrichthyans and some placoderms the anastomosis of the two canals is behind the nostrils. In fossil dipnoans such as *Holodipterus* (BMNH P.52566) the ethmoid commissure connects the two supraorbital canals rather than the two infraorbital canals as it does in actinopterygians, chondrichthyans and some placoderms. The former condition must be regarded as secondary and in part due to the interruption of the infraorbital sensory canal by the choana in dipnoans and primitive tetrapods.

In osteichthyans there is a further series of bones associated with the roof of the nasal region, the internasals or postrostrals. These are anamestic bones, variable in number and arrangement. In actinopterygians these elements occur only in long-snouted forms such as *Acipenser* (where there are more than twelve internasals), *Polyodon*, *Chondrosteus* and *Saurichthys* (where there is a single pair of extremely long bones). In actinistians the internasals form a median series of five or more in *Diplocercides* (Stensiö 1937), two or more in *Latimeria*, and one in *Rhabdoderma* (Forey 1981). In dipnoans there may be a single median internasal, as in *Fleurantia* (Graham-Smith & Westoll 1937), *Ceratodus* and *Neoceratodus*, long paired internasals, as in *Griphognathus* (Miles 1977: fig. 111), *Holodipterus* and *Scaumenacia* (Holmgren & Stensiö 1936), or an irregular series, as in *Dipnorhynchus*, *Uranolophus* (Denison 1968, 1969) and *Chirodipterus* (Miles 1977). In osteolepids, *Megalichthys* (Thomson 1964) has a single internasal, *Osteolepis* (Jarvik 1948) two median internasals, *Panderichthys* (Vorobjeva 1973) four and *Eusthenopteron* one large median internasal and five smaller anterior ones. The porolepid *Holoptychius* (Jarvik 1972: fig. 35) has an irregular series of eight to fourteen internasals. A small median internasal is present in *Ichthyostega* (Jarvik 1952) and loxommatids, but in no other tetrapod. From this we may conclude that internasals are primitively present in sarcopterygians but absent in actinopterygians.

Finally, there is one further series of bones associated with the nasal region in osteichthyans, the tectals, which are not canal-bearing and form a series lateral to the nasals and dorsal to the nostrils. Tectals are present in osteolepids (*Eusthenopteron*, *Osteolepis*), actinistians (*Rhabdoderma*, *Latimeria*), porolepids (*Holoptychius*) and dipnoans (*Dipnorhynchus*, *Chirodipterus*), but absent in actinopterygians. Thus I conclude that tectals are a synapomorphy of sarcopterygians.

Parasphenoid and associated toothplates

The parasphenoid is without a stalk (posterior elongation below the otic region) in the Gogo palaeoniscids and this is considered primitive for osteichthyans and placoderms.

Mimia toombsi

The parasphenoid is shown in lateral view in Fig. 13 and in ventral view in Fig. 50. It is a broad bone, of roughly rectangular shape, with a pectinate anterior margin. A median tongue of bone extends from this anterior margin to terminate between the vomers posterior to the paired openings of the ventral nasobasal canals. Behind the basiptyergoid process the parasphenoid is produced into a short, posterolaterally-directed arm which passes up towards the oticosphenoid fissure. Occasionally, as in BMNH P.53247 (Fig. 50), one of these arms may project back below and behind the spiracular canal, but this projection is not an ascending process in the strict sense (Gardiner & Bartram 1977: 231). A short median posterior extension ends at the level of the ventral fissure or occasionally a short distance in front of it. Posteriorly this extension is not applied to the basisphenoid and in this respect it is similar to that of *Australosomus* (Nielsen 1949: fig. 26). The buccal surface is completely covered by teeth, apart from two notches which delimit the posterolateral arms from the medial portion. The smooth areas around these notches (osubc, Fig. 50) probably mark the points of insertion of the subcephalic muscles (Nelson 1970a: 468). On the dorsal surface at the level of the basiptyergoid process the parasphenoid is produced into a small cup around the wide bucco-hypophysial canal (see *Moythomasia*, bhc, Fig. 52). The bucco-hypophysial canal passes through the centre of ossification. From the ventral opening of the bucco-hypophysial canal paired spiracular grooves (Fig. 50; see also *Moythomasia*, spig, Fig. 51) pass back towards the oticosphenoid fissure.

There is no dermal basiptyergoid process (anterior ascending process) and in this respect *Mimia* resembles *Cheirolepis*. The efferent pseudobranchial artery passed in between the parasphenoid and the basisphenoid (fepsa, Fig. 50).

A paired toothplate is associated with the parasphenoid in *Mimia*. It is an elongate, ovoid plate, rounded anteriorly but more pointed posteriorly, which fits between the edge of the parasphenoid and the entopterygoid, overlapping the latter. This paired bone (Av, Fig. 53) is

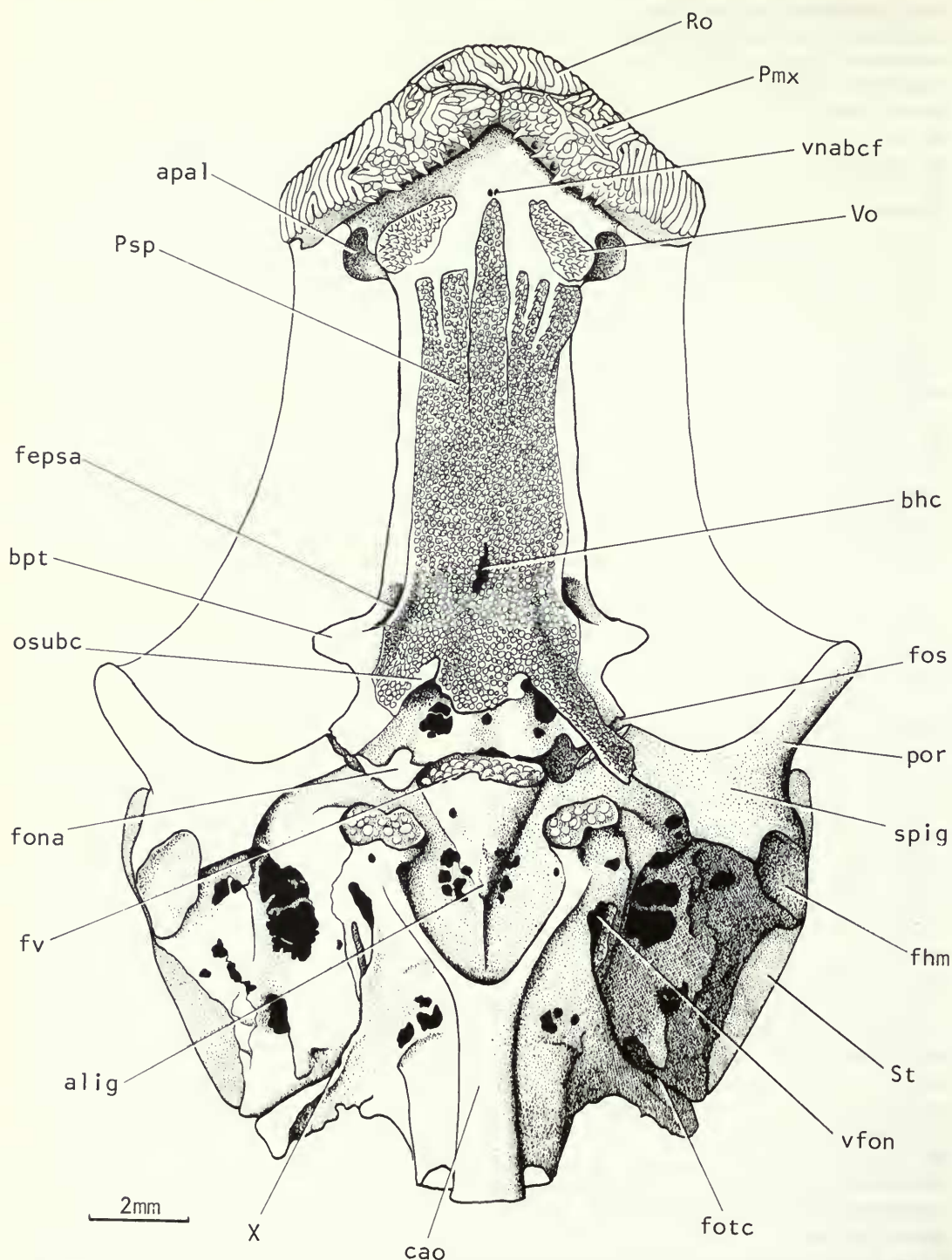


Fig. 50 *Mimia toombsi* Gardiner & Bartram. Restoration of braincase in ventral view, based on BMNH P.56496 and P.53247. From Gardiner & Bartram (1977).

shallowly concave dorsally and its entire oral surface is covered with closely-set, small teeth similar to those on the parasphenoid. It covers the toothless zone between the lateral edge of the parasphenoid and the adjoining part of the entopterygoid. It stretches from the foramen for the efferent pseudobranchial artery to just behind the vomer (Vo, Fig. 50). I will call it an accessory vomerine toothplate. An almost identical pair of toothplates occurs in *Moythomasia* and *Pteronisculus* (Nielsen 1942: fig. 34, Vo); a narrower, smaller pair has been described in *Australosomus* (Nielsen 1949: fig. 26). It is probable that these toothplates are widespread in the palaeoniscids.

Moythomasia durgaringa

The parasphenoid (Figs 7, 51, 52) is more extensive than in *Mimia*. Anteriorly it reaches the lateral margins of the basisphenoid and posteriorly not only extends to the level of the ventral fissures but also bears rudimentary ascending processes (asp, Fig. 7). Its toothed area, however, is less extensive than in *Mimia* and in front of the bucco-hypophysial canal only the central third of the bone is toothed. Anteriorly the median tongue of bone is little longer than the paired lateral ones and terminates at the level of the posterior margins of the vomers.

Behind the foramen for the efferent pseudobranchial artery the parasphenoid of one specimen (BMNH P.53221) continues out for a short distance onto the basiptyergoid process on one side only, but this can hardly be considered to be a true dermal basiptyergoid process (anterior ascending process). Posteriorly the posterolateral arm extends up onto the corner of the prootic forming an ascending process (or posterior ascending process) which terminates level with the bottom of the jugular canal. The ascending process, like the rest of the area behind the basiptyergoid processes, is covered with teeth which are never as large as those in front of the bucco-hypophysial canal. The spiracular groove (spig, Fig. 51) which passes back on the oral surface from the bucco-hypophysial canal extends onto the ascending process. Posteriorly the parasphenoid is spear-shaped, with a shallow, smooth ledge forming the hindmost margin. Between this spear-shaped portion and the ascending process is a distinct notch (gic, Fig. 51). The outer border of this notch is smooth (osubc) and presumably served for the insertion of the subcephalic muscle.

Immediately behind the parasphenoid in the roof of the mouth there is a pair of parotic toothplates (Gardiner & Bartram 1977: 240). These plates fill the area between the back of the parasphenoid and the aortic canal and underlie the ventral otic fissure. They are approximately rectangular in outline, with a more rounded anterior margin where they fit onto the ledge at the back of the parasphenoid. The left-hand plate has a narrow smooth ledge along its medial margin where it is overlapped by its partner. Both plates are covered in tubercular teeth, similar to those on the hind end of the parasphenoid. There is also a pair of accessory vomerine toothplates identical to those described in *Mimia*.

Parasphenoid: summary and discussion

The simplest form of actinopterygian parasphenoid is that seen in *Mimia* and *Cheirolepis* (Pearson & Westoll 1979), where it consists of a short, relatively broad toothed plate without a posterior stem or stalk and with no basiptyergoid process (anterior ascending process), and in which the ascending process (posterior ascending process) does not extend across the oticosphenoid fissure onto the lateral commissure. It is further characterized by the presence of a spiracular groove on its buccal surface which terminates at or near the bucco-hypophysial canal.

A similar type of parasphenoid (without posterior stem or basiptyergoid process, and where the ascending process does not reach the lateral commissure) is found in the rhipidistians *Eusthenopteron* (Jarvik 1954: fig. 18) and *Ectosteorhachis* (Romer 1937: fig. 4), the actinistians *Nesides* (Stensiö 1963b: fig. 45), *Wimania* (Bjerring 1967: pl. 2B) and *Latimeria* (Millot & Anthony 1958), the dipnoans *Uranolophus* (Denison 1968: fig. 8) and *Dipnorhynchus* (Thomson & Campbell 1971: fig. 25), porolepids such as *Glyptolepis* and *Holoptychius* (Jarvik 1954: figs 19, 20), and the youngolepidids (Chang 1982). The structure called basiptyergoid process in porolepids by Miles (1977: 159) is little more than the edge of the notch made by the

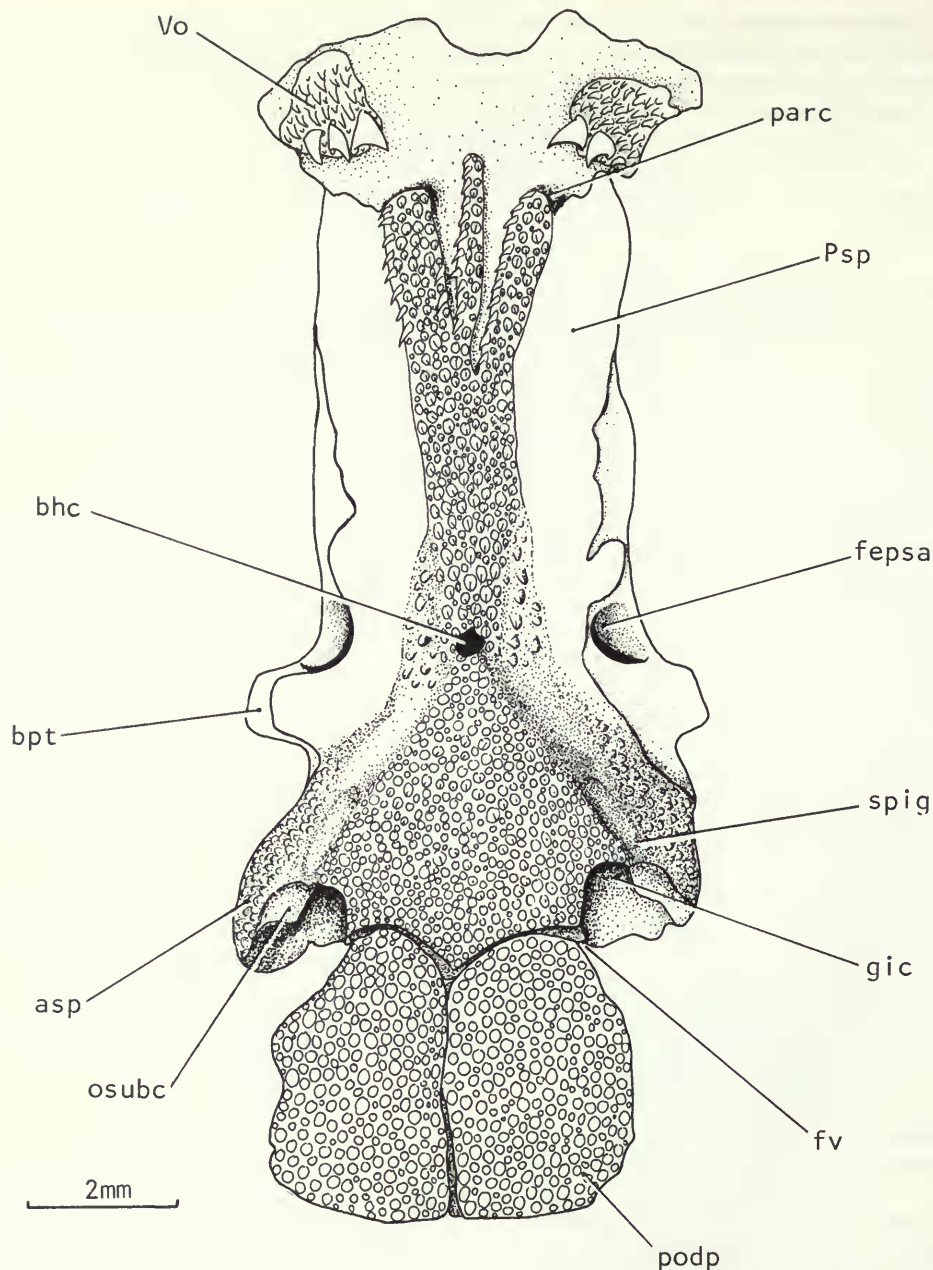


Fig. 51 *Moythomasia durgaringa* Gardiner & Bartram. Parasphenoid and associated structures in ventral view, from BMNH P.53221. After Gardiner & Bartram (1977).

passage of the efferent pseudobranchial artery. The spiracular groove (seen in *Moythomasia*, *porolepids*, *Youngolepis* and *Eusthenopteron*) is not present in actinistians or dipnoans, but its distribution in other osteichthyans and its presence on the neurocranium of *Acanthodes* (Miles 1973a) suggests it is a primitive osteichthyan feature. Thus the parasphenoid of *Moythomasia* and *Cheirolepis* must exemplify both the primitive actinopterygian and osteichthyan conditions. The posterior elongation of the parasphenoid in post-Devonian actinopterygians has been

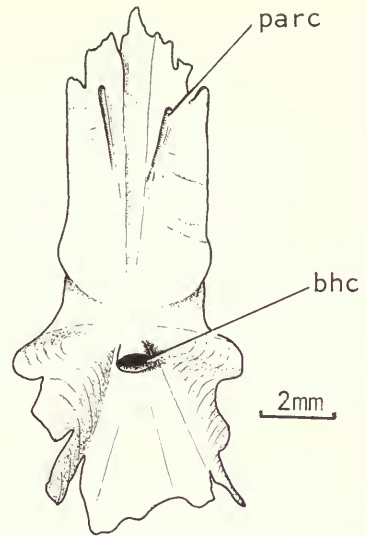


Fig. 52 *Moythomasia durgaringa* Gardiner & Bartram. Parasphenoid in dorsal view, from BMNH P.53217.

dealt with in detail by Gardiner (1973: 116), Patterson (1975: 527) and Miles (1977: 158), all of whom agree that elongation is the result of differential growth in phylogeny and that such a process occurred independently within the actinopterygians and dipnoans. In most post-Devonian palaeoniscids and in pholidopleurids this posterior extension never crossed the ventral otic fissure, but with the increase in size of the myodome the fissure came to lie further posteriorly (Gardiner & Bartram 1977: fig. 8) and consequently a short rounded stem developed behind the ascending process (*Pteronisculus*, Nielsen 1942; *Kentuckia*, Rayner 1951; *Boreosomus*, Nielsen 1942; 'Ambodipia', Beltan 1968; *Kansasiella*, Poplin 1974; *Coccolepis*, BMNH P.50822; *Australosomus*, Nielsen 1949). In other actinopterygians the stem of the parasphenoid is longer and extends across the fissure onto the ventral surface of the basioccipital (*Perleidus*, *Pachycormus*, parasemionotids, pholidophorids, Patterson 1975: 528). In *Polypterus*, living chondrosteans, *Paleopsephurus*, *Errolichthys* (Lehman 1952), *Chondrosteus* (RSM 1887.15.2), *Saurichthys* (Stensiö 1925), *Birgeria* (Nielsen 1949), pycnodonts, semionotids, caturids, *Amia*, *Lepisosteus* and most extant teleosts (Patterson 1975: 528) the parasphenoid floors the entire basioccipital and terminates beneath the occipital condyle. Similarly in *Bobasatrania* (Nielsen 1952) the parasphenoid extends back almost to the hind end of the neurocranium. The interrelationships of these actinopterygians possessing long-stemmed parasphenoids imply that the condition has been independently acquired on at least four occasions: in *Polypterus*, in *Birgeria*, in *Chondrosteus*, *Paleopsephurus* and living chondrosteans, and in neopterygians. A long stem has also been acquired on perhaps two other occasions: once in dipnoans (no stem in the Lower Devonian *Uranolophus*, Denison 1968) and possibly once within tetrapods (there is no stem in *Ichthyostega* according to Jarvik 1952; 1955: fig. 8).

1. *Parabasal canal*. Primitively in actinopterygians (and placoderms) neither the internal carotid nor the efferent pseudobranchial arteries pierced the parasphenoid. Instead the internal carotid artery entered the neurocranium behind the parasphenoid (in the short-stemmed forms) and passed forward between the parasphenoid and the basisphenoid in a short parabasal canal (*Cheirolepis*, *Mimia*, *Moythomasia*, *Pteronisculus*, *Australosomus*, etc.). The efferent pseudobranchial artery passed in above the parasphenoid and occasionally notched its lateral margin (*Mimia*, *Moythomasia*). In *Mimia* and *Moythomasia* the parabasal canal commences just behind the spiracular groove and a canal with precisely the same morphological relationships is also found in *Polypterus*, in the porolepid *Glyptolepis* (Jarvik 1972: fig. 19, cd.a.pal) and in *Youngolepis* (Chang 1982: fig. 7, c.a.ci). In *Glyptolepis*, however, the internal carotids passed

through the short stem of the parasphenoid into the parabasal canal through a foramen interpreted by Jarvik (1972: fig. 31) as having transmitted a medial branch of the internal carotid artery (see Gardiner 1973: 118). Anterior to the spiracular groove in *Glyptolepis* (prespiracular groove of Jarvik 1954, 1972; Bjerring 1971; but see Patterson 1975: 534; Gardiner & Bartram 1977: 243) and *Youngolepis* (Chang 1982: fig. 8B) the parasphenoid is notched by the passage of the efferent pseudobranchial artery (Gross 1936: 10A), though in some species of *Glyptolepis* (Jarvik 1972: fig. 31) this artery passed through the edge of the bone. A parabasal canal is also present in *Neoceratodus* (Holmgren & Stensiö 1936: fig. 288), *Griphognathus* (Miles 1977: fig. 50, c.i.?), fig. 56) and tetrapods (*Cryptobranchus*), and in dipnoans the efferent pseudobranchial artery enters the canal after passing in above the edge of the parasphenoid. A parabasal canal must therefore have been primitively present in osteichthyans and its subsequent loss in living chondrosteans, *Saurichthys*, *Latimeria* and *Eusthenopteron* (Jarvik 1954: fig. 6A, c.a.c.i) may be correlated with the narrowness of the parasphenoid in each of these fishes. A parabasal canal is not found in placoderms and is presumed to be a synapomorphy of osteichthyans.

2. *Internal carotid artery.* The backward growth of the parasphenoid in more advanced actinopterygians had a marked effect on the course of the internal carotids and associated arteries and at least four different topographies may be recognized (Gardiner 1973: 116).

In *Polypterus* the posterior stem of the parasphenoid is not only below the carotid arteries, but also below the dorsal arterial system and this condition is unique. In *Birgeria*, *Saurichthys*, *Saurorhynchus*, *Errolichthys*, *Chondrosteus* and *Paleopsephurus* a parabasal canal is missing and the stem of the parasphenoid as well as the ascending processes must have been above the carotid arteries as in *Acipenser*. In saurichthyids (Stensiö 1925; Gardiner 1960: fig. 21) and *Chondrosteus* (RSM 1887.15.2) there is a large, paired foramen in the parasphenoid beneath the posterior margin of the ascending process; this presumably transmitted the orbital artery (as originally suggested by Stensiö) and not the common carotid as Gardiner (1973: 116) and Patterson (1975: 331) have supposed. In *Lepisosteus* and *Amia* the efferent pseudobranchial and internal carotid arteries pass through notches in the lateral edges of the parasphenoid, into the parabasal canal (as in *Pteronisculus*, *Perleidus*, parasemionotids, caturids and *Lepidotes*) and the stem of the parasphenoid lies between the internal carotids. However, the internal carotid artery in *Boreosomus*, unlike all other described palaeoniscids, passed through a foramen in the base of the ascending process. This is a variation of the last condition. In *Dapedium*, pholidophorids, leptolepids and other primitive teleosts (Patterson 1975: 532) there are foramina in the parasphenoid for both the internal carotid and efferent pseudobranchial arteries and it appears that in these fishes the notches seen in more primitive forms such as *Perleidus*, parasemionotids, caturids and *Lepidotes* have become foramina, probably as a result of growth of the lateral edges of the parasphenoid. Conditions are similar in the porolepid *Glyptolepis* (Jarvik 1972: fig. 31). In advanced dipnoans the stem of the parasphenoid lies between the internal carotid artery and above the efferent pseudobranchial artery, much as in *Amia* and *Lepisosteus*. A similar relationship has been achieved in such tetrapods as *Cryptobranchus*, although here the carotid artery passes through a foramen in the lateral edge of the parasphenoid.

3. *Basipterygoid process.* An endoskeletal basipterygoid process is present in chondrichthyans, acanthodians and osteichthyans and is considered primitive for gnathostomes.

Primitively the osteichthyan skull possessed a well-developed endoskeletal basipterygoid process (*Mimia*, *Cheirolepis*, *Nesides*, *Glyptolepis*, *Eusthenopteron*, *Youngolepis*) but only in later, more advanced actinopterygians did it acquire support from the parasphenoid. Although the lateral angle of the parasphenoid in dipnoans may be in a similar topographic position to the actinopterygian dermal basipterygoid process, there is no reason to consider it homologous as Miles (1977: 159) has done. A dermal basipterygoid process is an actinopterygian specialization, possibly developed to reinforce the ventral wall of the myodome as originally suggested by Rayner (1951: 81). In the more primitive palaeoniscids and chondrosteans a dermal basipterygoid process is lacking (*Cheirolepis*, *Mimia*, *Moythomasia*, *Polypterus*, *Acipenser*,

Polyodon, *Chondrosteus*, *Saurichthys*, *Errollichthys*, *Birgeria*), while in *Polypterus*, *Birgeria* and *Saurichthys* the endoskeletal basipterygoid process has also been reduced or lost.

A dermal basipterygoid process is first observed in some of the more advanced palaeoniscids and their relatives. Though small in *Boreosomus*, *Platysomus* and *Perleidus*, it is extensive in *Pteronisculus*, *Cosmoptychius* and *Kansasiella* (Poplin 1974: fig. 8) where the endoskeletal and dermal components are about equal. A similarly well developed dermal basipterygoid process, with a stout endoskeletal component above, is also present in *Dapedium* (Patterson 1975: fig. 112) and *Lepisosteus*, but in some caturids the process is very small (*Heterolepidotus*, *Caturus chirotes*, Rayner 1948: fig. 7) and in others it is absent (*Caturus furcatus*, '*Aspidorhynchus*', *Macrepistius*). The basipterygoid process (dermal and endoskeletal) has also been lost in amioids, pachycormids and most Recent teleosts. By contrast in *Pholidophorus bechei* and *Lepidotes* (Patterson 1975: 529) the dermal basipterygoid process is very large and the endoskeletal part almost vestigial. In other pholidophorids and leptolepids the basipterygoid process is entirely dermal; a similar massive dermal process is found in a few other teleosts such as *Diplomystus*, osteoglossoids and ichthyodectids.

In summary, the endoskeletal basipterygoid process has been lost on several occasions; in *Polypterus*, in *Birgeria* and *Saurichthys*, in *Australosomus*, in caturids and amiids, in pachycormids and in later teleosts. The dermal basipterygoid process must also have been lost on more than one occasion (amiids, pachycormids and several teleosts groups).

4. *Ascending process.* This is another important outgrowth of the parasphenoid in actinopterygians, developed primarily in relation to the spiracular diverticulum and which reinforces the outer wall of the myodome. Such an ascending process (or posterior ascending process) is a specialized feature developed within the group. Primitively in osteichthyans it was very short and did not extend across the ventral otic fissure in *Mimia* and *Cheirolepis*, porolepids (*Glyptolepis*, Gross 1936: pl. 8), youngolepidids (Chang 1982: fig. 7), osteolepids (*Eusthenopteron*, Jarvik 1954: fig. 18) and Devonian actinistians (*Diplocercides*, Bjerring 1972: fig. 3A). Only in later actinopterygians and *Polypterus* is a long ascending process developed.

There has been considerable confusion over the identification of the ascending process. Stensiö (1925: 85) called the ascending process on the parasphenoid of sturgeons and *Saurichthys* the 'processus ascendens posterior', but homologized the same process in *Amia* and *Lepisosteus* with the dermal basipterygoid process of palaeoniscids and so called it the 'processus ascendens anterior'. The view that the ascending process in *Amia* is not comparable to that in *Acipenser* received support from Pehrson (1940: 38) and Holmgren (1943: 39), but Nielsen (1942: 106; 1949: 84) and Rayner (1951: 81) demonstrated that the two are strictly homologous. Jarvik (1954: 51) considered the ascending process of the rhipidistian and actinistian parasphenoid to be the homologue of the basipterygoid process of the parasphenoid in *Pteronisculus*, referring to it as the anterior ascending process. But as Patterson (1975: 533) and Gardiner & Bartram (1977: 243) have shown, it is homologous with the ascending process of primitive actinopterygians.

A true ascending process (one which crosses the oticosphenoid fissure) is first met with in *Moythomasia* and *Kentuckia*, where the slender process extends onto the lateral commissure but terminates level with the bottom of the jugular canal. In more advanced palaeoniscids such as *Kansasiella*, *Pteronisculus*, *Boreosomus* and in *Australosomus* the ascending process is more extensive and its tip approaches or enters the lower opening of the spiracular canal. In *Polypterus*, where the spiracle is unstricted, the ascending process is large and very complicated (Jarvik 1954) and may be assumed to have had a different history from that of *Birgeria*, *Saurichthys* and living chondrosteans, where it covers a major part of the otic and orbitotemporal walls.

In more advanced actinopterygians such as *Perleidus*, parasemionotids, semionotids and caturids (Patterson 1975: 533) the ascending process, though as extensive as in most palaeoniscids, is less stout and often more distinctly grooved by the spiracular diverticulum. The ascending process in pholidophorids, leptolepids (Patterson 1975: 519), pachycormids (Patterson 1975: fig. 106) and *Ichthyokentema* (Patterson 1975: fig. 150) on the other hand is shorter and terminates below the spiracular canal when the latter is present. The ascending process in most Recent teleosts is also

short, but occasionally it is enlarged and meets the frontal as in *Gasterosteus* and *Arapaima*. Patterson (1975: 534) has suggested that the ascending process may be reduced in height in teleosts as a result of the reduction in the spiracular diverticulum. Whether or not this is true, there is little doubt that the ascending process has developed on at least two occasions within actinopterygians, once in *Polypterus* and once in the actinoptेरans.

The spiracular grooves on the ascending processes of *Moythomasia* are continued onto the ventral surface of the parasphenoid (Fig. 51), where they join around the lower opening of the bucco-hypophysial canal on a level with the efferent pseudobranchial foramina. The spiracular grooves are linked by a transverse groove in *Pholidophorus bechei* and the Sinemurian *Leptolepis* (Patterson 1975: figs 62, 143). A corresponding groove is found in the porolepids *Holoptychius* (Gross 1936: fig. 10A), *Glyptolepis* (Jarvik 1972: fig. 31) and *Porolepis* (Jarvik 1972: pl. 9), and in *Youngolepis* (Chang 1982: fig. 8). Teeth occur in the spiracular groove of *Moythomasia* (Fig. 51), some specimens of *Pteronisculus*, *Perleidus* (Patterson 1975: fig. 115) and on the ventral plate of the ascending process in the mouth of the spiracular cleft in *Polypterus*. Teeth are also present in the transverse groove in *Moythomasia*, *Glyptolepis* and *Youngolepis*. Some confusion has resulted from the misidentification of this transverse groove in rhipidistians, where it has been designated 'prespiracular' by Jarvik (1954, 1972) and Bjerring (1971, 1977), but as Patterson (1975: 534) and Gardiner & Bartram (1977: 243) have demonstrated, the groove is homologous with that in actinopterygians and is therefore a spiracular groove. Although it is absent in dipnoans and actinistians, the occurrence of this groove in actinopterygians, porolepiforms and youngolepidids suggests that it is a primitive osteichthyan character.

A similar transverse groove is present on the parasphenoid of placoderms (Kulkzycki 1956: pl. 1G; Miles & Westoll 1968: fig. 18a; White & Toombs 1972: figs 5, 6, 7; Young 1979: pl. 5). This has been variously interpreted as having housed blood vessels (Kulkzycki 1956: 107; Stensiö 1963a: 122) or outgrowths of the hypophysial stalk (White & Toombs 1972: 388). Nevertheless, it bears the same relationship to the bucco-hypophysial canal as in many osteichthyans and the presence of teeth along its borders (White & Toombs 1972: fig. 5) suggests it is a spiracular groove.

5. Parasphenoid teeth. The entire oral surface of the parasphenoid is toothed in *Mimia* (Fig. 50) and *Cheirolepis*. In *Moythomasia*, however, although the posterior region is completely toothed, anterior to the lower opening of the bucco-hypophysial canal the teeth are confined to a narrow, central band (Fig. 51). In *Polypterus* teeth occupy the full width of the parasphenoid anteriorly, but beneath the orbit they are restricted to a narrow band similar in extent to that in *Moythomasia*. Posteriorly this band separates into two curved bands of teeth which run along the anterior edges of the ventral plate of the ascending process (Allis 1922: fig. 9). In most other palaeoniscids, parasemionotids and the majority of caturids the parasphenoid is toothed from the level of the ascending process forwards. Reduction and loss of parasphenoid teeth has occurred on several occasions within the actinopterygians. Thus the teeth are reduced to a small tooth patch around the lower opening of the bucco-hypophysial canal in *Saurichthys* and are completely wanting in *Birgeria*, *Chondrosteus* and living chondrosteans. Parasphenoid teeth are also missing in *Australosomus*, *Bobasatrania*, pycnodonts, *Macrepistius*, *Ichthyokentema*, *Catervariolus* and most teleosts (Patterson 1975: 529).

In Devonian and Carboniferous actinistians and in *Eusthenopteron* the parasphenoid has a tooth-bearing median ridge which extends back to enclose the lower opening of the bucco-hypophysial canal. In later actinistians and in some osteolepids (*Ectosteorhachis*, *Megalichthys*) the tooth-bearing ridge is confined to the area in front of the bucco-hypophysial canal. In *Youngolepis* (Chang 1982: fig. 8) the parasphenoid is completely toothed but in porolepids such as *Glyptolepis* (Jarvik 1972: fig. 31) the tooth patch is restricted to the area around the opening of the bucco-hypophysial canal and, as in *Elops*, there are in addition numerous small toothplates in the roof of the oral cavity. In *Porolepis* (Jarvik 1972: fig. 65), however, the teeth are reduced to a median row of some eight large teeth borne on a raised area; parallel enlargement and specialization of parasphenoid teeth is seen in various teleosts (e.g. albulids, hiodontids, osteoglossids).

In the Lower Devonian dipnoan *Uranolophus* (Denison 1968: fig. 8) the buccal surface of the parasphenoid is toothed except posteriorly where there is a small area of smooth bone, whereas in the other Lower Devonian form (*Dipnorhynchus*) the buccal surface has a continuous dentine covering (Campbell & Barwick 1982). In many dipnoans with a stalked parasphenoid the buccal surface is covered with teeth whereas the posterior stem is smooth (*Griphognathus*, *Holodipterus* Miles 1977: 151, 154). In *Dipterus valenciennesi* (White 1965) the bucco-hypophysial duct opens in the anterior portion of this toothed area. In *Conchopoma* the toothed anterior portion is expanded and opposed to the median basibranchial toothplate (Denison 1969: 199), but in *Chirodipterus* (Miles 1977: 153) the parasphenoid teeth have been entirely lost.

In placoderms the parasphenoid may be completely covered by numerous small teeth as in *Buchanosteus* (White & Toombs 1972: fig. 5; Young 1979: pl. 5) and *Kujdanowiaspis* (Jarvik 1954: fig. 34).

Primitively, therefore, in osteichthyans and placoderms the oral surface of the parasphenoid was toothed.

6. *Bucco-hypophysial canal*. The bucco-hypophysial duct opens through the parasphenoid into the roof of the mouth in primitive actinopterygians (*Mimia*, *Moythomasia*, *Cheirolepis*, *Polypterus*, *Saurichthys*, *Chondrosteus*, *Perleidus*), and this opening is retained in more advanced forms such as '*Aspidorhynchus*', *Dapedium*, *Lepidotes*, *Caturus*, *Heterolepidotus* and *Elops* (Patterson 1975: 530).

An open bucco-hypophysial duct is also characteristic of most actinistians (*Nesides*, *Latimeria*), all described porolepids (Jarvik 1972), and *Youngolepis* (Chang 1982), *Eusthenopteron* (Jarvik 1954), *Dipterus* and *Ichthyostega* (Säve-Söderbergh 1932). In *Glyptolepis* (Jarvik 1972: fig. 19D) the opening is paired.

The parasphenoid also contains an open bucco-hypophysial canal in placoderms. White & Toombs (1972: fig. 6) figured a paired opening for the bucco-hypophysial canal in *Buchanosteus*, but Young (1979: fig. 17; pl. 5) has shown, in better preserved material, that the opening, although bilobed, is single.

The striking similarity between the placoderm and osteichthyan parasphenoids (teeth, spiracular grooves, and foramen for bucco-hypophysial canal) suggests that a parasphenoid is a synapomorphy of a group containing osteichthyans and placoderms.

7. *Subcephalic muscles*. Nelson (1970a: 468) has suggested that the subcephalic muscles of *Latimeria*, which extend beneath the intracranial joint from the otico-occipital to the parasphenoid, may be derived from one or more of the anterior body myomeres such as occur in *Polypterus*. In *Polypterus* the body musculature extends forwards beneath the occipital and otic regions, to be inserted on the parasphenoid immediately behind the ascending process. It thus spans the ventral otic fissure which lies above the parasphenoid. The area of muscle insertion lies between the posterior margin of the ascending process and the stem of the parasphenoid.

A distinct notch is present in the posterior margin of the parasphenoid in *Mimia* and *Moythomasia*, in the latter immediately behind the ascending process, and below and anterior to the articulation for the first infrapharyngobranchial; it may be inferred that subcephalic muscles of the type found in *Polypterus* were inserted in this region (osubc, Figs 50, 51). This notch may also be identified by the same topographic and morphological criteria as have been used to recognize the insertion of the subcephalic muscles in rhipidistians and actinistians (Bjerring 1967, 1971; Jarvik 1966, 1972).

Bjerring (1971: fig. 6), however, taking *Latimeria* as his model, has restored subcephalic muscles in *Pteronisculus* inserting on the hind end of the parasphenoid, but originating on the underside of the basioccipital in the triangular area circumscribed by the grooves for the lateral dorsal aortae (and thereby spanning the ventral otic fissure as in *Latimeria*). Patterson (1975: 538) suggested that although such an area on the basioccipital could well have served for muscle attachment it does not follow that the muscles were directed forwards and proposed that it was more likely that it served for the attachment of anterior trunk muscles, serially homologous with those attaching to the back of the parasphenoid in *Polypterus*. In my opinion this triangular area

of the basioccipital (primitive for actinopterygians; Patterson 1973: 558) never served for muscle attachment in actinopterygians. It lies above the general level of the floor of the occipital region in *Mimia* (Fig. 13), *Moythomasia* (Fig. 7) and *Kentuckia* (Rayner 1951: fig. 9); it never shows any sign of muscle scars, is frequently fenestrated (Figs 14, 15, 50) and in *Moythomasia* (Fig. 51) the paired parotic toothplates neatly fill in the area between the back of the parasphenoid and the aortic canal. Furthermore this triangular area, although domed in *Mimia* and *Moythomasia*, is depressed and smooth in *Pteronisculus* (Nielsen 1942: fig. 6) and *Kentuckia* (Rayner 1951: fig. 9). Thus it appears that a subcephalic muscle of rhipidistian type originating on the underside of the occipital ossification did not exist in actinopterygians, and I suggest that the foremost trunk myomere inserted on the posterior part of the parasphenoid only, as in *Polypterus*, and not on the underside of the occipital ossification.

Distinct pits in a similar position to the notches in *Mimia* and *Moythomasia* occur on the underside of the parasphenoid of *Cosmoptychius* (Schaeffer 1971: fig. 8A) and *Coccolepis* (BMNH P.50822), immediately behind the bucco-hypophysial canal and medial to the internal carotid foramen. There is a pair of pits in this position in several more advanced actinopterans including *Heterolepidotus*, *Caturus chiotes* (Gardiner 1960: fig. 36, eff.pseud.), *Lepidotes latifrons*, *Pholidophorus bechei* and *Ichthyokentema* (Patterson 1975: 535; figs 62, 150). In other pholidophorids, leptolepids and pachycormids the pits are more posteriorly placed. Thus I conclude that subcephalic muscles of the type found in *Polypterus* were primitively present in actinopterygians and inserted on the posterior part of the parasphenoid. Identically-placed pits to those seen in *Cosmoptychius* and *Pholidophorus* occur in the osteolepids *Megalichthys*, *Ectosteorhachis* (Romer 1937: fig. 4, ci), *Eusthenodon* (Bjerring 1967: pl. 2C) and *Eus-thenopteron* (Bjerring 1967: pl. 2A), but there is no reason to assume that the muscles inserting in these pits were more like those of *Latimeria* than of *Polypterus*, particularly since the area of muscle insertion in *Latimeria* is far in advance of the bucco-hypophysial canal.

In other actinopterygians such as *Perleidus* and parasemionotids there is a much wider, irregular recess (Patterson 1975: 536; figs 98, 116) for the subcephalic muscles; this condition is paralleled by the porolepids *Glyptolepis* and *Porolepis* (Jarvik 1972: 86) and by *Youngolepis* (Chang 1982: figs 7, 8), where there is a similar recess behind the spiracular groove, implying a broad insertion. This has prompted Patterson (1975: 538) to postulate that a broad insertion may be the primitive condition.

8. *Accessory toothplates*. In *Mimia* (Av, Fig. 53), *Moythomasia*, *Elonichthys* (Watson 1925: fig. 22, D.Pt₁), *Pteronisculus* (Nielsen 1942: fig. 34) and *Australosomus* (Nielsen 1949: fig. 26) there is a large toothplate between the entopterygoid and parasphenoid (see p. 271), which I have termed the 'accessory vomerine toothplate'. The occurrence of such a toothplate is considered primitive for actinopterygians.

In chondrichthyans there is a shagreen of small denticles in the skin of the roof of the mouth (Nelson 1970b: 2) and in the porolepid *Glyptolepis* (Jarvik 1972: figs 8C, D, 16, 22, 30) there are numerous small dental plates. Similarly in *Elops* (Nybelin 1968) there is a small patch of toothplates lying free in the mucous membrane in the region of the bucco-hypophysial canal. Thus primitively in gnathostomes there must have been numerous small dental plates in the skin lining the roof of the mouth. In early actinopterygians some of these are presumed to have been replaced by a single accessory vomerine toothplate.

Paired toothplates also occur in the roof of the mouth immediately behind the short parasphenoid of primitive osteichthyans. These paired parotic plates are found in *Moythomasia* (Fig. 51) and *Eus-thenopteron* (Jarvik 1954: fig. 22).

Palatoquadrate and dermal bones of the cheek

Mimia toombsi

In *Mimia* the palatoquadrate is very long; anteriorly it articulates with the lateral ethmoid (apal, Fig. 50) while its posterior part reaches beyond the occiput (Fig. 55). In the majority of specimens the palatoquadrate is ossified throughout as one bone, as in the larger specimens of

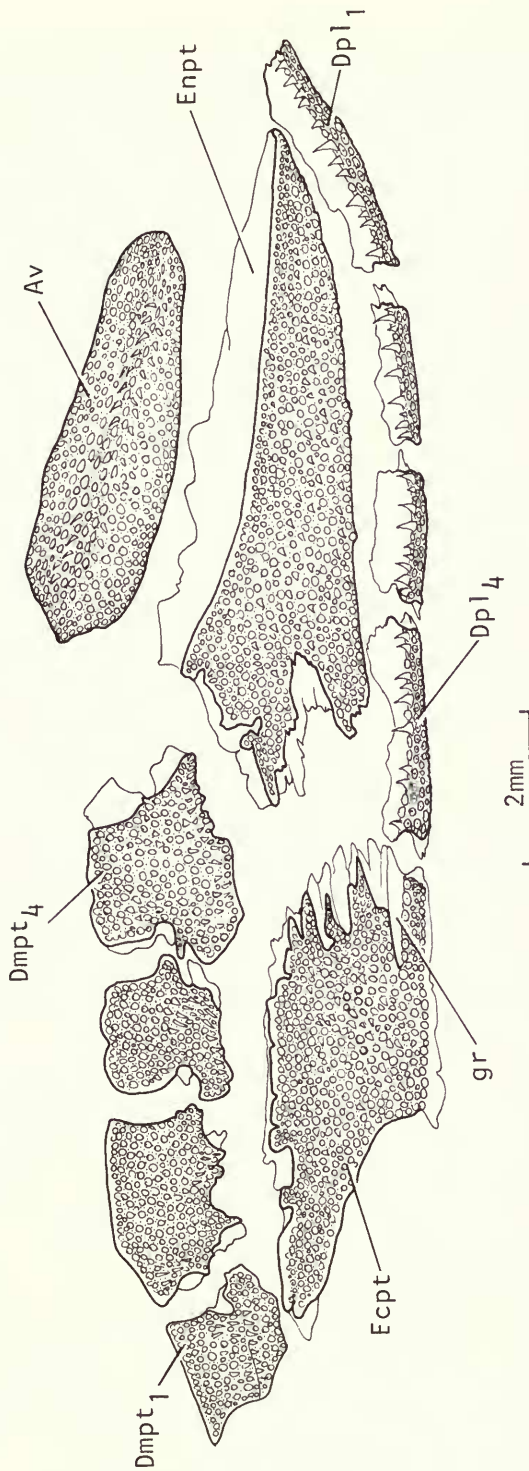


Fig. 53 *Mimia toombsi* Gardiner & Bartram. Dermal bones of the left palate of an incompletely ossified individual in medial view, from BMNH P.56473.

Pteronisculus and *Australosomus* (Nielsen 1942: 143; 1949: 99) and as in specimens of *Eusthenopteron* and *Glyptolepis* (Jarvik 1954: 27; 1972: 70). In all these specimens it is impossible to detect ossification centres. Two smaller specimens of *Mimia*, however, show three separate ossifications: one in the quadrate region (Fig. 57), one in the metapterygoid region and one in the autopalatine region; these three ossifications were separated in life by a large area of cartilage. In one or two other specimens the junctions between these bones may be inferred.

The quadrate appears to have been the most prominent ossification in the palatoquadrate cartilage, with its centre of ossification in the condyle region. The quadrate forms the inner margin of the adductor mandibulae fossa, and reaches anterodorsally to the level of the hole for the basiptyergoid process. Here it meets the much smaller autopalatine ossification, the junction being marked by a prominent ridge. The centre of ossification of the metapterygoid lies dorsally around the fossa for the levator arcus palatini muscle and ventrally this bone extends to just below the spiracular groove (spig, Fig. 56). Anteriorly the metapterygoid forms the posterior margin of the hole for the basiptyergoid process, the anterior margin being formed by the autopalatine. Thus the quadrate is the largest endoskeletal ossification, the metapterygoid is somewhat smaller and the autopalatine considerably less extensive. In this respect *Mimia* resembles *Acanthodes* (Miles 1965: fig. 1).

The palatoquadrate ossification is roughly triangular in its outline with a circular hole (hbpt, Fig. 56) in the anterodorsal margin. During life the basiptyergoid process slid through this hole which functioned as a guide during lateral movements of the palatoquadrate. A similar hole has been described in the palate of certain species of *Pteronisculus* and *Boreosomus* by Lehman (1952: figs 35, 57) and in the palate of *Kentuckia* by Rayner (1951: fig. 3), but unlike *Pteronisculus* (Nielsen 1942: fig. 35) and *Kentuckia* there is no additional process on the palate in this region.

The posterior division of the palatoquadrate forms a high, nearly vertical plate which is curved dorsally so that its anterolateral face is concave in a dorsoventral and a rostrocaudal direction and its medial face is correspondingly convex. The concavity in the anterior face of the

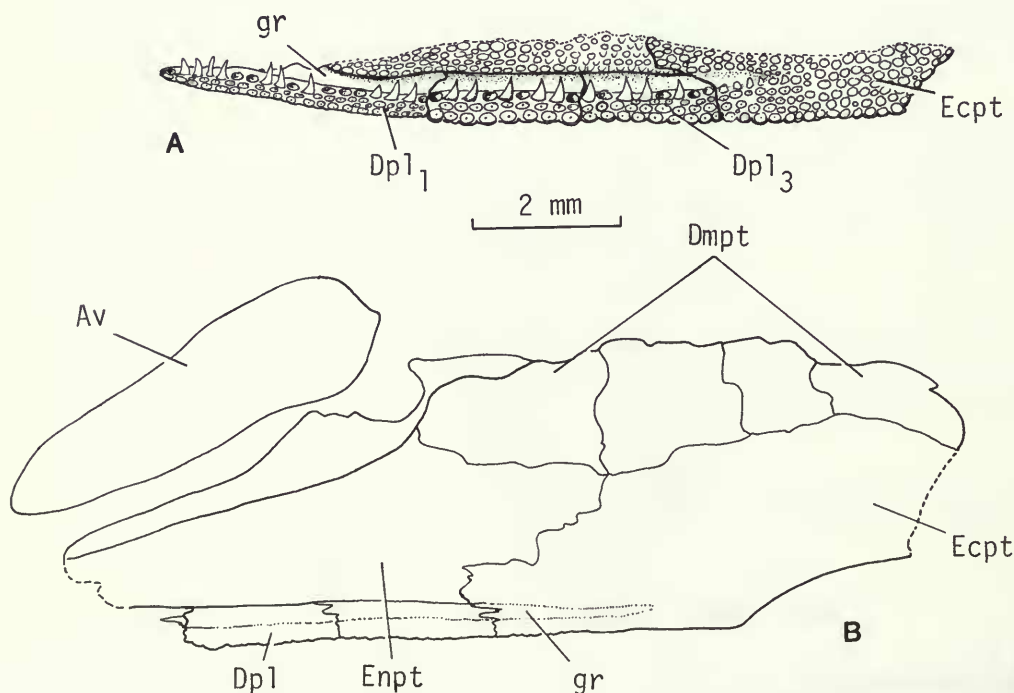


Fig. 54 *Mimia toombsi* Gardiner & Bartram. Dermal bones of the right palate in medial view. (A), from BMNH P.56490; (B), from BMNH P.56486.

metapterygoid (lapf, Fig. 56) presumably served for the insertion of the levator arcus palatini muscle. A similar concavity is recognizable in *Pteronisculus* and *Australosomus* (Nielsen 1942: 144; 1949: 102). The whole of the posterior margin of the palatoquadrate is in contact with the medial face of the preopercular and ventrally with the medial face of the quadratojugal (Fig. 57). This junction is often so complete that the preopercular and quadratojugal are immovably fixed to the palatoquadrate (Fig. 60). Ventrally the palatoquadrate forms the medial boundary of the opening for the adductor mandibulae, but anterior to this fossa it is in contact with the medial face of the ventral part of the maxilla. As with the preopercular, the junction is often so complete that the maxilla is fused to the palatoquadrate. This junction is further strengthened by fusion of the dermopalatines with both the overlying palatoquadrate and the maxilla (Figs 56, 60).

In the metapterygoid region there is a gradual transition between the dorsal, laterally bent part and the vertical or quadrate part of the palatoquadrate ossification, but there is no distinct angle between these two regions as there is in *Pteronisculus* (Nielsen 1942: 145). On the medial side of the metapterygoid region there is a conspicuous groove running back from the hole for the basipterygoid process down onto the quadrate (spig, Figs 56, 57). A similar groove has been figured in *Pteronisculus* (Nielsen 1942: figs 35, 36). Gardiner (1973: fig. 8, icg) originally attributed this groove to the internal carotid artery, but from its position just dorsal to the tooth-bearing sheet of dermal bone it is more probable that it represents the lateral surface of the ventral end of the spiracular diverticulum. A similar groove on the parasphenoid (spig, Fig. 50) is apparently a continuation of the groove on the metapterygoid. In *Porolepis* and *Eusthenopteron* (Jarvik 1954: fig. 16, resh) there is a similar groove on the palate which has been called the spiraculo-hyomandibular recess by Jarvik, and as in *Mimia* and *Pteronisculus* this groove is in the same position as the posterior division of the spiracular slit in *Polypterus*.

The posterodorsally-facing margin of the palatoquadrate ossification is pierced by several short transverse canals. In the metapterygoid and in the dorsal region of the quadrate there are two such canals (fmand.int. VII, Figs 55, 56, 57), while ventrally in the quadrate there is either a single canal or a pair of canals immediately above the condyles (fmand.int. VII, Fig. 57). These canals presumably transmitted the internal mandibular branch of the facial nerve as in *Polypterus* (Allis 1922: 282), the dorsal pair of foramina serving for the entrance of that nerve and the ventral pair for its exit. A single short transverse canal and groove has also been described in *Pygopterus* (Aldinger 1937: 145) and *Pteronisculus* (Nielsen 1942: 145). Lateral to the posterior end of the spiracular groove and immediately above these transverse canals lay the hyomandibula with the interhyal beneath it (Hy, Ih, Fig. 55); ventrally the quadrate articulated with the lower jaw by a double-headed joint, the facets or condyles of which lie lateral to one another as in *Pteronisculus* (Nielsen 1942: fig. 33) and *Eusthenopteron* (Jarvik 1954: fig. 25).

That part of the palatoquadrate ossification in front of the point of junction with the basipterygoid process is mostly formed by the autopalatine. This forms a thin plate of bone, concave dorsolaterally and convex ventromedially. Posteriorly the limit of the autopalatine is marked by a distinct ridge behind which there is a somewhat deeper concavity in the lateral surface. This concavity immediately in front of the hole for the basipterygoid process marks the most anterior insertion point of the adductor mandibulae muscle. Anteriorly the autopalatine turns inwards to articulate with the lateral ethmoid by a cartilaginous interface.

Like the cartilage bones, in most specimens the dermal toothplates on the medial surface of the palatoquadrate are ossified throughout as one bone, and closely resemble those of *Eusthenopteron* (Jarvik 1954: fig. 16), except that in the latter there are separate dermopalatines. In two specimens, however, individual bones are apparent: in one there are nine and in the other ten (Fig. 53), four dermometapterygoids, an entopterygoid, an ectopterygoid and three or four dermopalatines.

The entopterygoid (Enpt, Figs 53, 54) is the largest of the dermal bones on the oral face of the palatoquadrate. It is approximately triangular in outline and tapers to a point anteriorly where it rests against the anterior end of the autopalatine. Like the pterygoid of *Eusthenopteron* and *Glyptolepis* (Jarvik 1972: fig. 25), in the adult it fuses indistinguishably with the underlying autopalatine and metapterygoid. However, neither the entopterygoid nor the underlying dermopalatine reach the anterior limit of the autopalatine. The entopterygoid is broadest

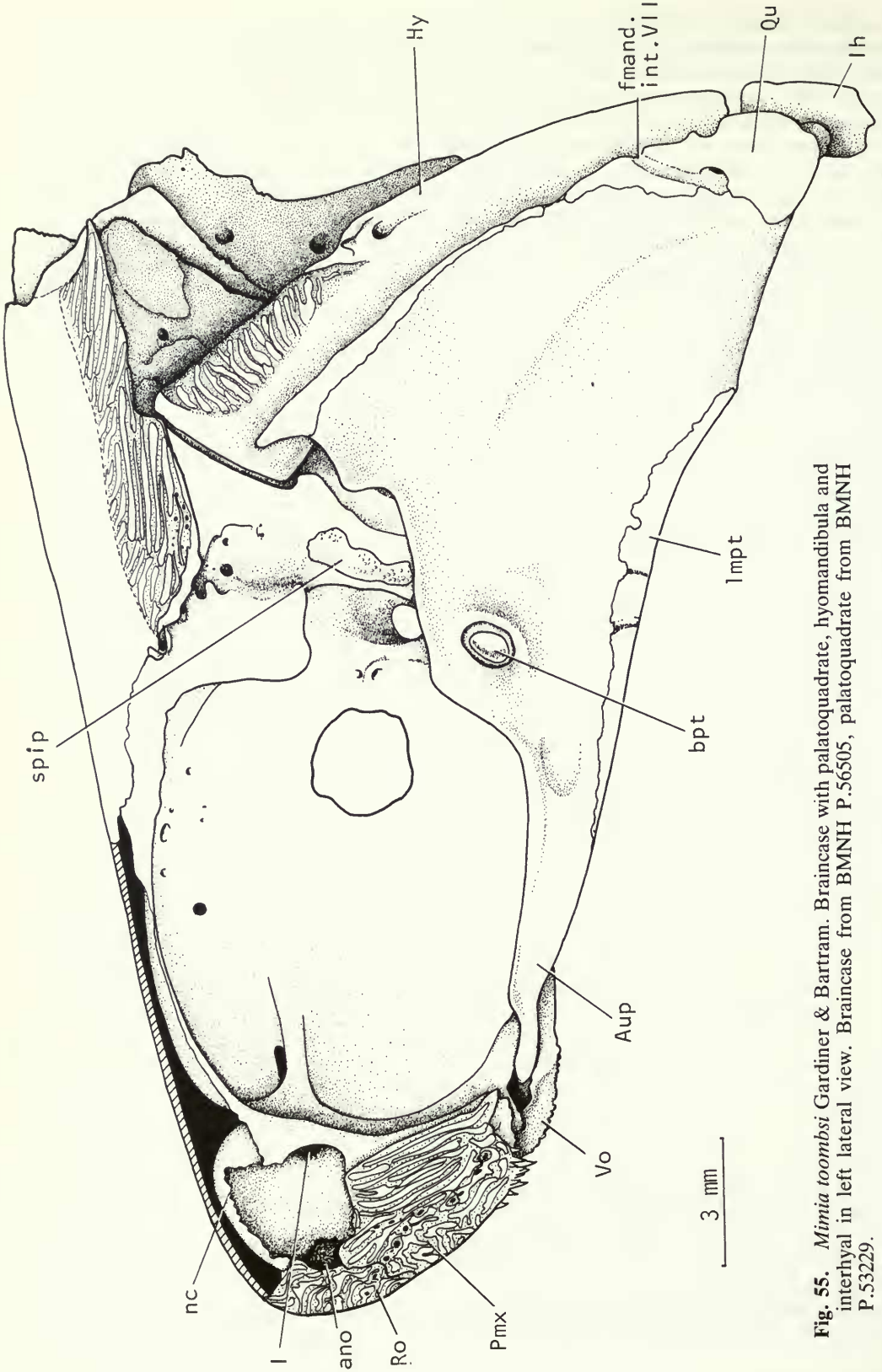


Fig. 55. *Minia toombsi* Gardiner & Bartram. Braincase with palatoquadrate, hyomandibula and interhyal in left lateral view. Braincase from BMNH P.56505, palatoquadrate from BMNH P.53229.

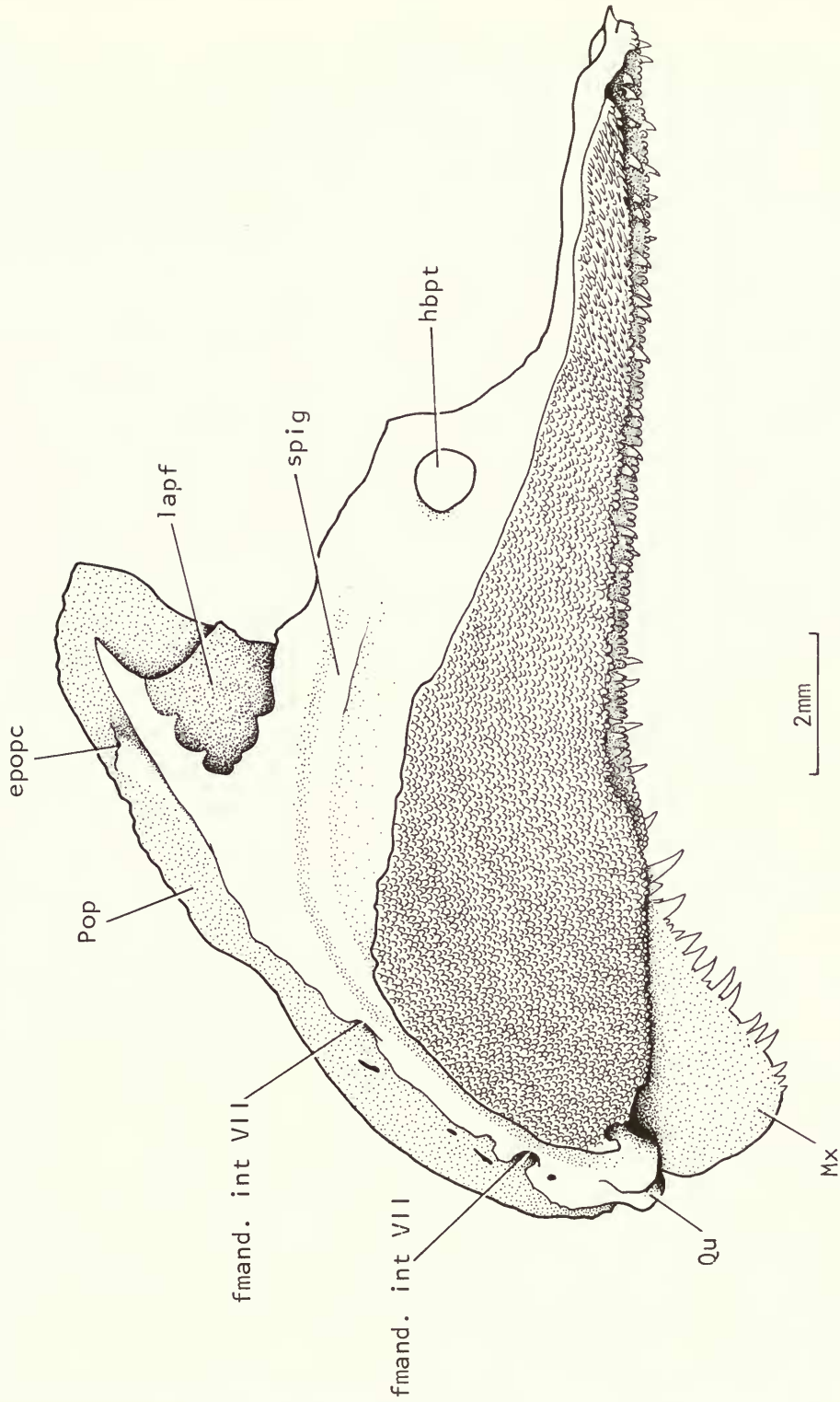


Fig. 56 *Mimia toombsi* Gardiner & Bartram. Left palatoquadrate and associated dermal bones in medial view, from BMNH P.56498.

posteriorly where it interdigitates with the ectopterygoid and the anteriormost dermometapterygoid. Medially it is covered by closely-set, small teeth, similar to those on the parasphenoid, except for a shelf-like margin of thin bone dorsally. Posteriorly this untoothed margin terminates in a small process (Fig. 53) which fits beneath the anterior margin of the hole for the basiptyergoid process. A similar anterior process on the anteriormost dermometapterygoid forms the hind margin of this hole. The accessory vomerine toothplate (Av, Figs 53, 54) fits loosely on this dorsal margin of the entopterygoid, spanning the gap between it and the parasphenoid. The radiation centre of the entopterygoid lies near the dorsomedial margin, but more posteriorly than in *Pteronisculus* (Nielsen 1942: fig. 37). Ventrally the entopterygoid adjoins the dermopalatines and covers a marginal zone of the oral face of these bones, but leaves a well-marked groove (gr, Figs 53, 54) between it and the dermopalatine tooth row.

There are four dermometapterygoids (Dmpt, Figs 53, 54) which rest against the medial face of the metapterygoid and quadrate, and in adult fish fuse indistinguishably with them and one another and with the ectopterygoid. The two anterior dermometapterygoids lie well below the spiracular groove, but the two posterior bones form the lateral edge of the spiracular gill slit. All four bones interdigitate with one another; the anteriormost also interdigitates with the entopterygoid while the three more posterior elements suture with the ectopterygoid ventrally. All three posterior bones are completely covered by small, closely set teeth.

The ectopterygoid (Ecpt, Figs 53, 54) covers the posteroventral part of the oral face of the palatoquadrate. Caudally the bone extends almost as far as the posterior dermometapterygoid, but rostrally it terminates before the basiptyergoid articulation and the anteriormost dermometapterygoid. Posteriorly the ectopterygoid lies against the vertical oral face of that part of the quadrate which bounds the adductor fossa. Immediately in front of the adductor opening the ventral part of the ectopterygoid is turned under and outwards to form an almost horizontal external lamina. This lamina sutures with the maxilla, overlapping a narrow marginal zone of the

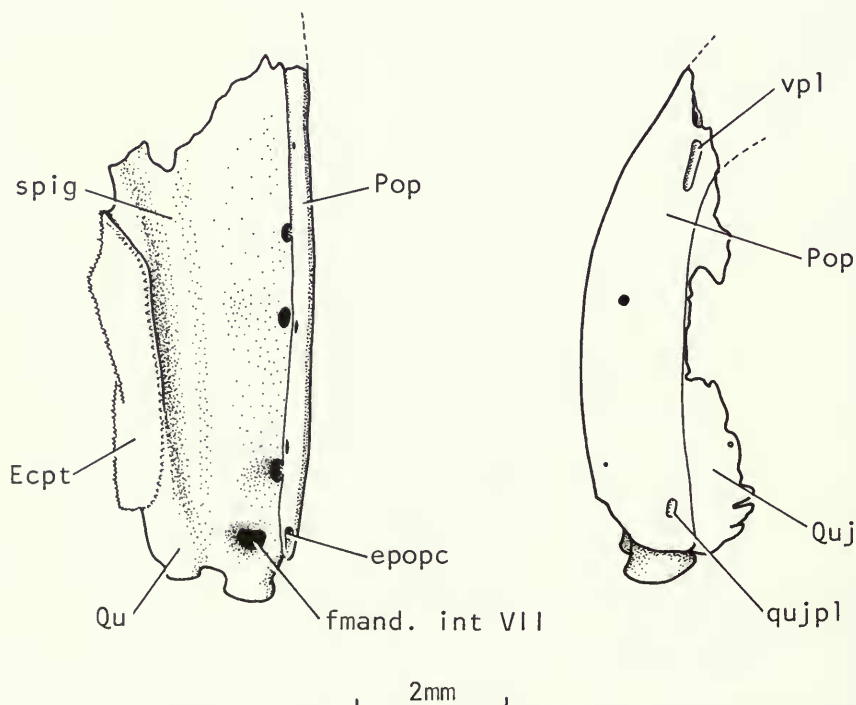


Fig. 57 *Mimia toombsi* Gardiner & Bartram. Quadrate region of palatoquadrate and associated dermal bones in posterior (left) and lateral views, from BMNH P.53254.

internal horizontal lamina. Anteriorly the ectopterygoid sutures with the posterior dermopalatine and the entopterygoid. The dorsal margin is sutured to the three posterior dermometapterygoids while the anterodorsal corner of the ectopterygoid just reaches the anteriormost dermometapterygoid. The entire oral face of the bone is covered by closely set, pointed teeth, apart from a narrow groove anteriorly (gr, Fig. 53). This groove is continuous with a similar groove in the dorsal margin of the dermopalatines (Fig. 54). The centre of ossification lies at the posteroventral corner, in front of the adductor opening where the ectopterygoid contacts the maxilla.

The dermopalatines form a series of three or four interdigitating bones which provide an anterior continuation of the horizontal external lamina of the ectopterygoid. The lateral margins of the dermopalatines overlap a narrow marginal zone of the internal horizontal lamina of the maxilla and their medial margins are overlapped orally by the entopterygoid. Laterally the dermopalatines are covered by small, closely set pointed teeth, medial to which is a series of much larger pointed teeth. The internal lamina beyond the tooth row is devoid of teeth and forms a well-marked groove (gr, Fig. 54) between the toothed area and the overlapping entopterygoid. The centre of ossification of each dermopalatine lies more or less at the middle of the bone.

The maxilla is of the usual palaeoniscid type (also seen in onychodonts, Jessen 1966) in which there is a narrow suborbital part and a high posterior expansion (Fig. 60). The suborbital portion is longer than in *Cheirolepis*, *Moythomasia* and *Pteronisculus*. The dorsal and posterior margins of the posterior expansion overlap a considerable portion of the lower margin of the quadratojugal (Fig. 63) so that only a small part of the quadratojugal is visible. The suborbital extension of the maxilla is overlapped by the posteroventral margin of the jugal and by the lachrymal. A horizontal longitudinal lamina stretches along the medial, ventral margin of the maxilla from the anterior margin of the adductor fossa to the anterior limit of the bone. The lamina increases in breadth as it passes anteriorly but narrows again from the level of the basiptyergoid process anteriorly. The maxilla is connected by its horizontal lamina with the ectopterygoid and dermopalatines, as in *Pteronisculus* (Nielsen 1942: fig. 35). The ventral edge of the palatoquadrate sits above this horizontal, longitudinal lamina and in the quadrate region is produced dorsally into a flattened flange (lmpt, Fig. 55) which is attached to the inner surface of the maxilla. This quadrate flange stretches from the adductor fossa to the posterior limit of the autopalatine and is intimately connected with the maxilla. Ventrally the free margin of the maxilla bears teeth; the largest teeth occur at the anterior end of the posterior expansion and the smallest posteriorly. An outer series of much smaller teeth grades almost imperceptibly into the surface ornamentation. The radiation centre of the maxilla lies above the horizontal lamina and just anterior to the expanded posterior region (see Fig. 66, *Moythomasia*).

The preopercular is a long, acutely angled bone which extends forwards above the posterior expansion of the maxilla and carries the preopercular canal which is directed towards the otic portion of the infraorbital canal (temporal canal). Its anteroventral margin overlaps the quadratojugal (Figs 60, 61, 63) to such an extent that this latter bone is difficult to recognize in lateral view. The preopercular canal does not run the whole length of the bone as it does in *Pteronisculus* (Nielsen 1942: fig. 27), but instead exits dorsally before reaching the anterodorsal margin (epopc, Figs 56, 63). The canal runs parallel to the posterodorsal margin, piercing the radiation centre. From close to the radiation centre the horizontal pit-line passes anteriorly towards the anterior margin of the preopercular. Internally, it is marked by a small but distinct branch of the preopercular canal (bpopc, Fig. 63). In some specimens a short vertical pit-line (vpl, Fig. 61) joins the horizontal pit-line posteriorly, but in others the two lines are separate (Fig. 62). The preopercular is thickened internally along the route of the preopercular canal and it is this region which is in intimate contact with the palatoquadrate. Both the metapterygoid and quadrate areas of the palatoquadrate contribute to this dorsoposterior flange (Fig. 55) which fuses with the inner surfaces of the preopercular and quadratojugal. This intimate contact of the palatoquadrate with the preopercular and quadratojugal dorsally and the maxilla ventrally, together with the strongly overlapping sutures between the maxilla, preopercular and quadratojugal, produces a rigid cheek unit (Gardiner 1967).

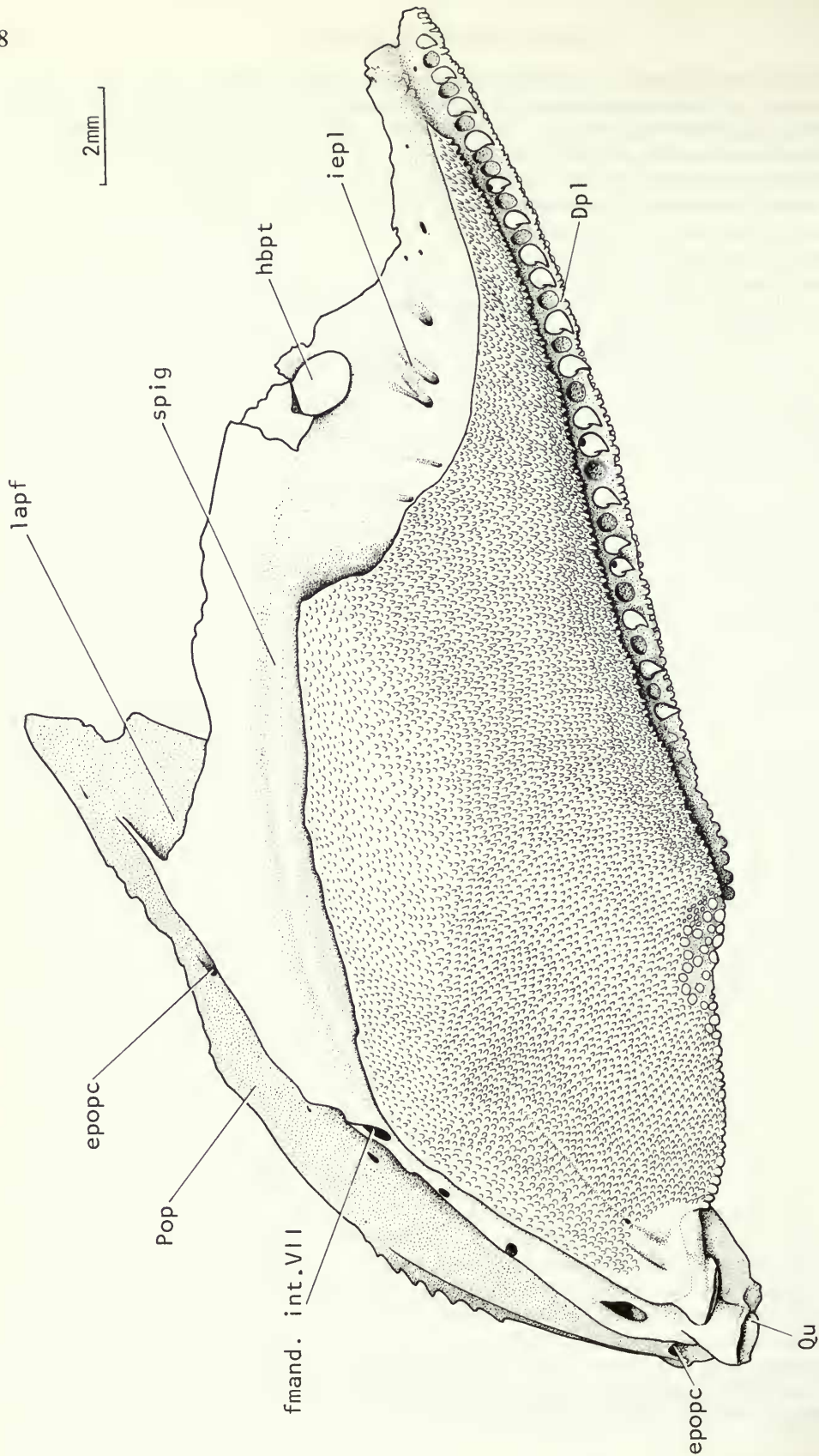


Fig. 58 *Moythomasia durgaringa* Gardiner & Bartram. Left palatoquadrate and associated dermal bones in mesial view, from BMNH P.53221.

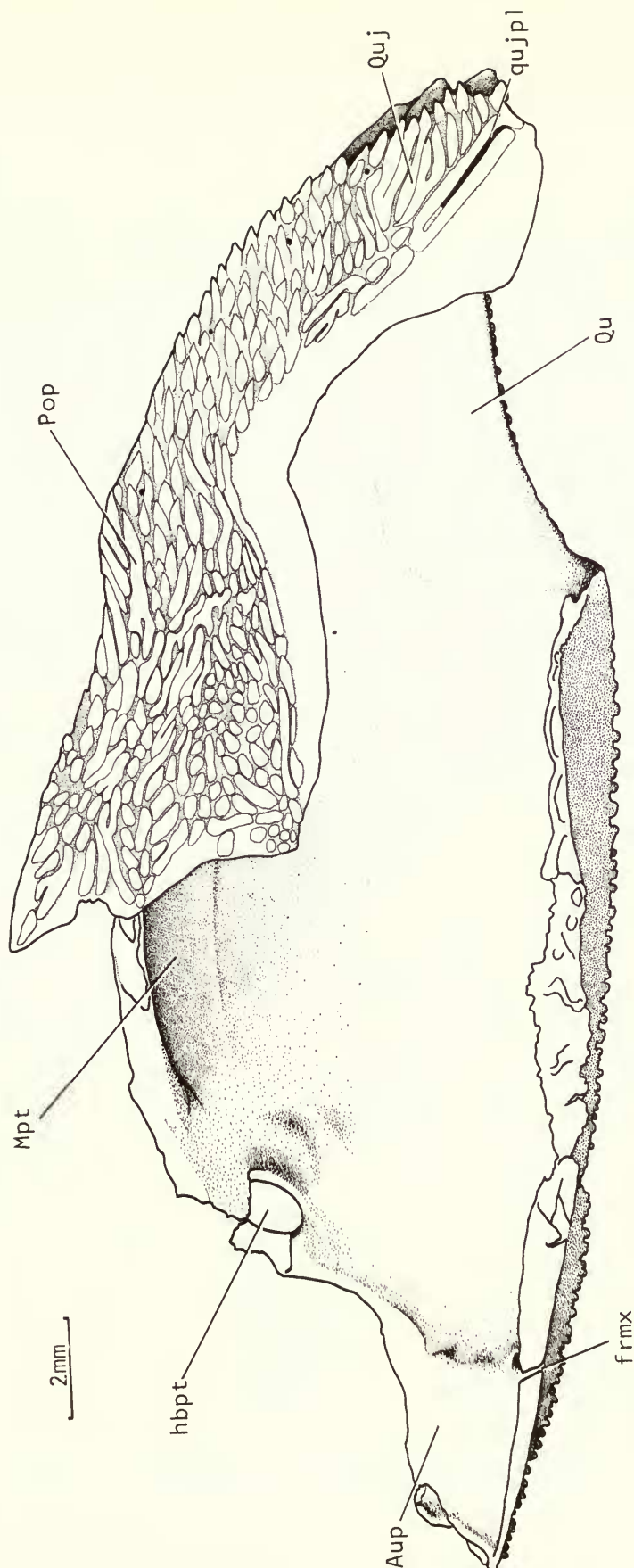


Fig. 59 *Moythomasia durgaringa* Gardiner & Bartram. Left palatoquadrate, preopercular and quadratojugal in lateral view, from BMNH P.53221.

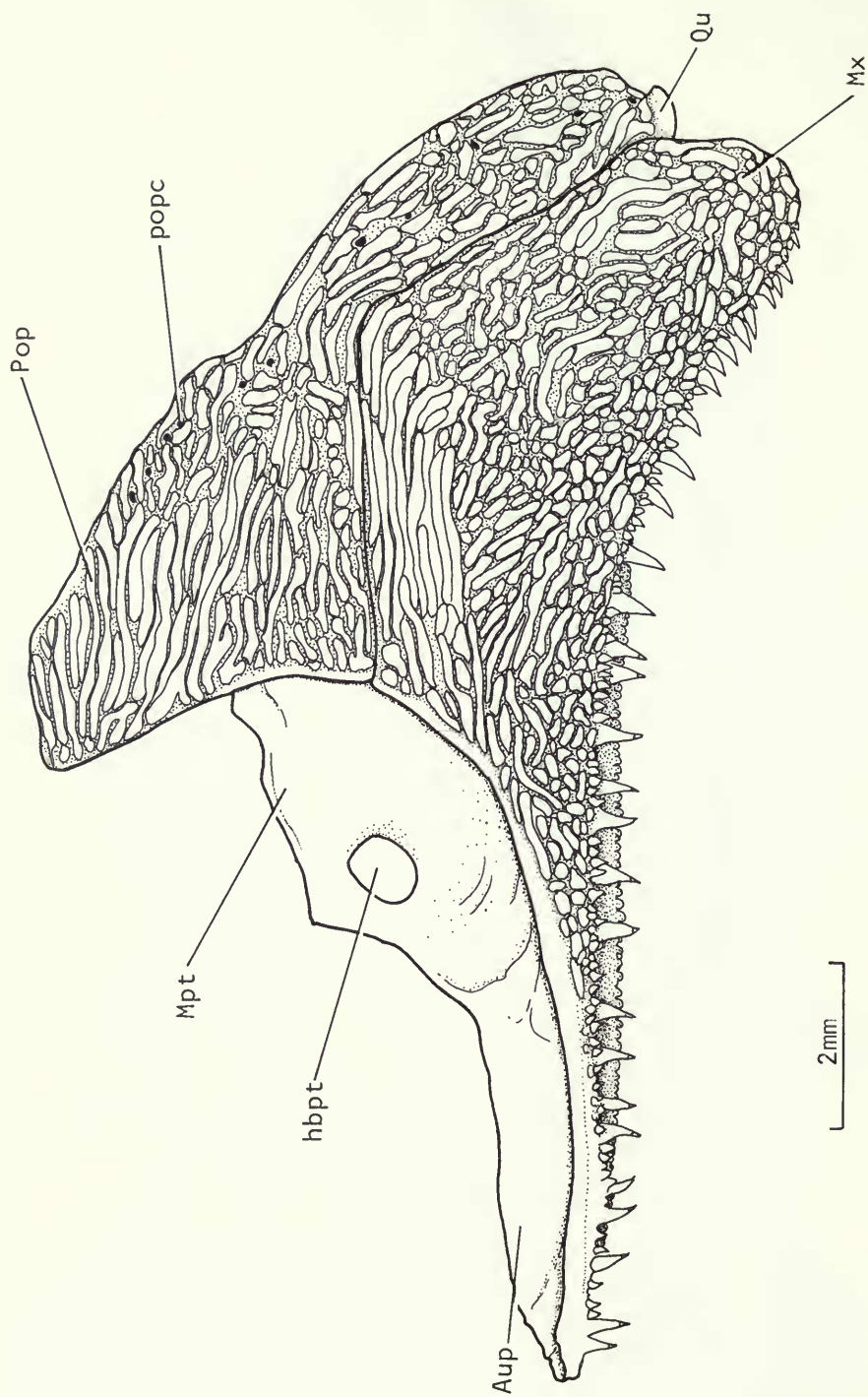


Fig. 60 *Minia toombsi* Gardiner & Bartram. Left palatoquadrate and associated dermal bones in lateral view, from BMNH P.56498.

The quadratojugal is overlapped dorsally by the preopercular and anteriorly by the maxilla and only a small portion of its surface is ornamented (Fig. 63). The radiation centre lies immediately anterior to the exposed, ornamented area beneath the pit-line. The quadratojugal pit-line, although short, is about the same length as the vertical pit-line and has at least three nerve foramina serving it.

The infraorbital series comprises three bones, the dermosphenotic, jugal and lachrymal. The dermosphenotic is considered here with the other cheek bones because it is in series with the infraorbital bones and is loosely attached or hinged to the skull roof.

The dermosphenotic is triangular in shape, sits over the top of the postorbital process and forms the anterolateral margin of the spiracular opening. The radiation centre is in the posterior third of the bone near its dorsal margin. The centre is pierced by the infraorbital canal which traverses it in a vertical direction. The infraorbital canal passes into the intertemporal anterior to the spiracular opening. A branch of the infraorbital canal passes anteriorly within the dermosphenotic to terminate blindly before reaching the anterior end of the bone. Ventrally the dermosphenotic is overlapped to a small degree by the anterodorsal margin of the jugal; anteriorly it may just make contact with the nasal and dorsally it contacts the frontal and intertemporal, resting on a ledge formed by the neurocranium. In some specimens it may also meet the anterior end of the supratemporal.

The jugal is the largest element of the infraorbital series. It has a convex posteroventral margin which overlaps the concave anterodorsal margins of the preopercular and maxilla. The course of the infraorbital canal changes from nearly vertical to nearly horizontal within the bone, the change of direction marking the radiation centre.

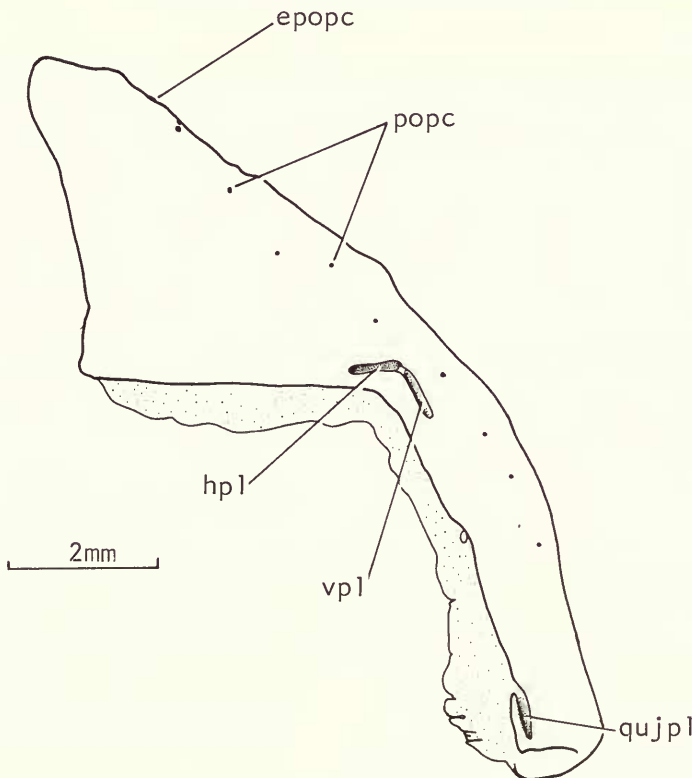


Fig. 61 *Mimia toombsi* Gardiner & Bartram. Sketch restoration of left preopercular and quadratojugal in lateral view, to show pit-lines.

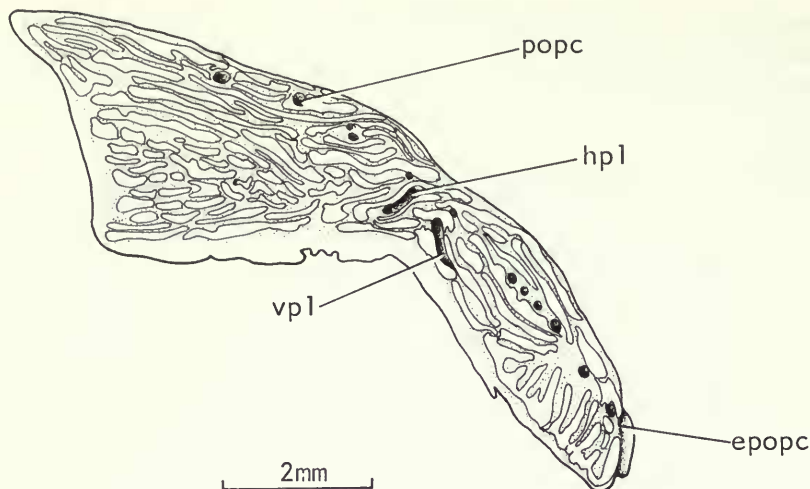


Fig. 62 *Mimia toombsi* Gardiner & Bartram. Left preopercular in lateral view, from BMNH P.56473.

The lachrymal is a short, thin ossification tapering to a point anteriorly. Posteriorly it overlaps the jugal while anteriorly it is overlapped by the premaxilla. The infraorbital sensory canals run the length of the bone and the centre of radiation lies near the posterior margin. The external openings of the sensory canal lie along its ventral margin.

Moythomasia durgaringa

The palatoquadrate in *Moythomasia* differs in proportions from that of *Mimia*. It has a much longer post-basipterygoid portion and a correspondingly shorter and stouter anterior section. In shape it more nearly resembles that of *Cheirolepis* (Pearson & Westoll 1979: figs 7, 8) than any other described palaeoniscid. In all specimens the palatoquadrate is a single ossification and it is difficult to detect individual ossification centres. The anterior end, which turns inwards to articulate with the lateral ethmoid, is much broader than in *Mimia*, as is the facet on the lateral ethmoid. The whole of the ventral margin in front of the adductor fossa is produced laterally into a flattened flange (Fig. 59) which is intimately attached to the inner surface of the maxilla above the horizontal longitudinal lamina (hll, Fig. 67). Anteriorly this flange is pierced by one or more nerve foramina (frm, Fig. 59) for branches of the maxillary nerve. As in *Mimia* there is a circular hole in the anterior dorsal margin (hbpt, Fig. 59) to accommodate the basipterygoid process. Beneath the hole on the medial surface of the palatoquadrate are several dorsally-directed pits (iepl, Fig. 58). By analogy with *Polypterus* these are presumed to have been insertion points for the ethmopalatine ligament (Allis 1922: 244). The posterolateral face of the palatoquadrate forms a broad flange which is in intimate contact with the preopercular and quadratojugal. This flange is pierced in its ventral half by four foramina. The dorsalmost of these foramina served for the entrance of the internal mandibular branch of the facial nerve and the ventralmost for its exit.

Like the cartilage bones, the dermal toothplates on the medial surface are ossified throughout as one bone. The toothplate is more extensive than in *Mimia* and forms much of the margin to the spiracular groove.

Laterally the dermopalatines are covered by small rounded teeth similar to those on the ventral ectopterygoid region. Medial to these is a series of much larger, pointed teeth, which show a similar replacement sequence to those on the maxilla and dentary. A well-marked groove separates this tooth row from the entopterygoid.

The maxilla has a shorter but much stouter postorbital portion than in *Mimia*. The teeth likewise are much stouter and less needle-like. At the centre of radiation of the maxilla several

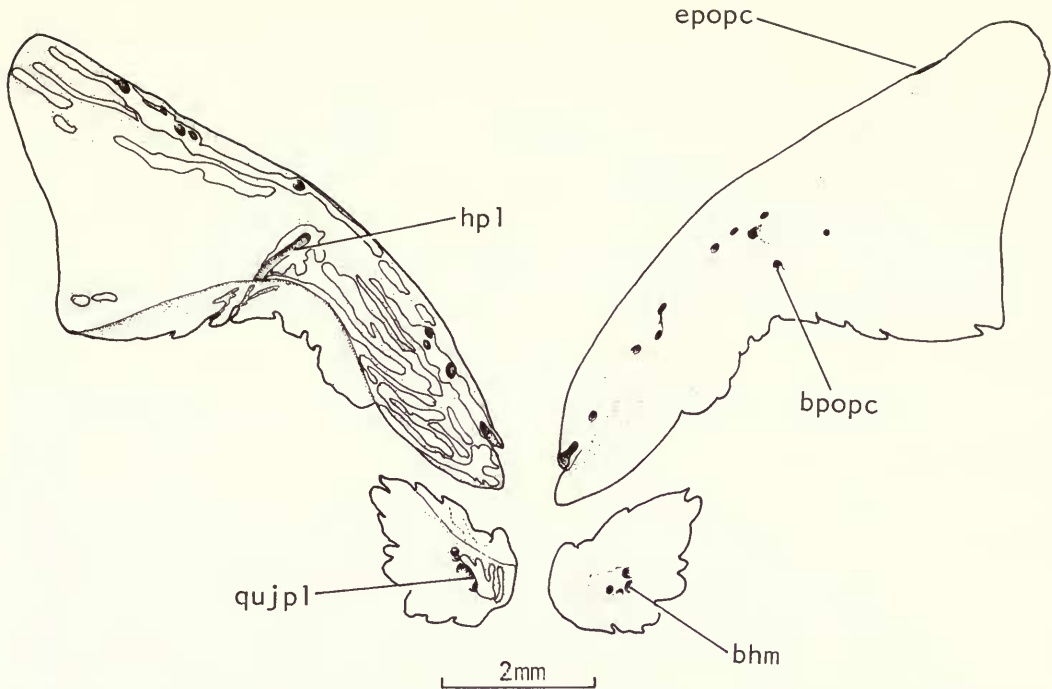


Fig. 63 *Mimia toombsi* Gardiner & Bartram. Left preopercular and quadratojugal in lateral (left) and medial views, from BMNH P.56484.

nerve foramina pass into the medial surface (bhm, Fig. 67), whereas externally a corresponding series of pits presumably housed the neuromasts of the anterior part of the horizontal pit-line (hpl, Fig. 66). An anterior continuation of the horizontal pit-line is also found on the maxilla of *Polypterus* (Jarvik 1947: fig. 1) and *Pteronisculus* (Nielsen 1942: pl. 9, fig. 1).

The preopercular is not so expanded dorsally as that of *Mimia* and the preopercular canal exits two-thirds of the way along the posterodorsal margin (epopc, Fig. 58).

The quadratojugal is stout and triangular and the pit-line makes a long slanting groove on its surface. Medially three nerve foramina transmitted fine branches of the mandibular nerve to the line.

The dermosphenotic is less extensive both anteriorly and ventrally than in *Mimia*. Anteriorly it tapers to a point and scarcely contacts the nasal. Posteroventrally it is overlapped by the jugal.

The jugal is more strongly convex posteriorly than in *Mimia* and the infraorbital canal opens by two sets of pores ventrally rather than a dorsal suite of pores as in *Mimia*.

The lachrymal is very different in shape from that of *Mimia*; much broader, and bifurcated anteriorly at the point of the exit of the infraorbital canal. Posteriorly the lachrymal overlaps the jugal, but anteriorly it overlaps the premaxilla. Anteroventrally the ornament closely resembles that on the ventral edge of the maxilla. A similar ornamentation is found on the posteroventral margin of the premaxilla and rostral. The infraorbital sensory canal enters and leaves the lachrymal through dorsally-directed pores (inc, Fig. 74). Beneath the canal several pores pass right through the bone (p, Fig. 74), as they do through the premaxilla.

Palatoquadrate: summary and discussion

1. *Palatoquadrate commissure and vomer*. In the ontogenetic development of actinopterygians and dipnoans the anterior ends of the palatoquadrates are joined by a blastema both to one another and to the overlying trabeculae (Holmgren 1943, Bertmar 1966). This blastema

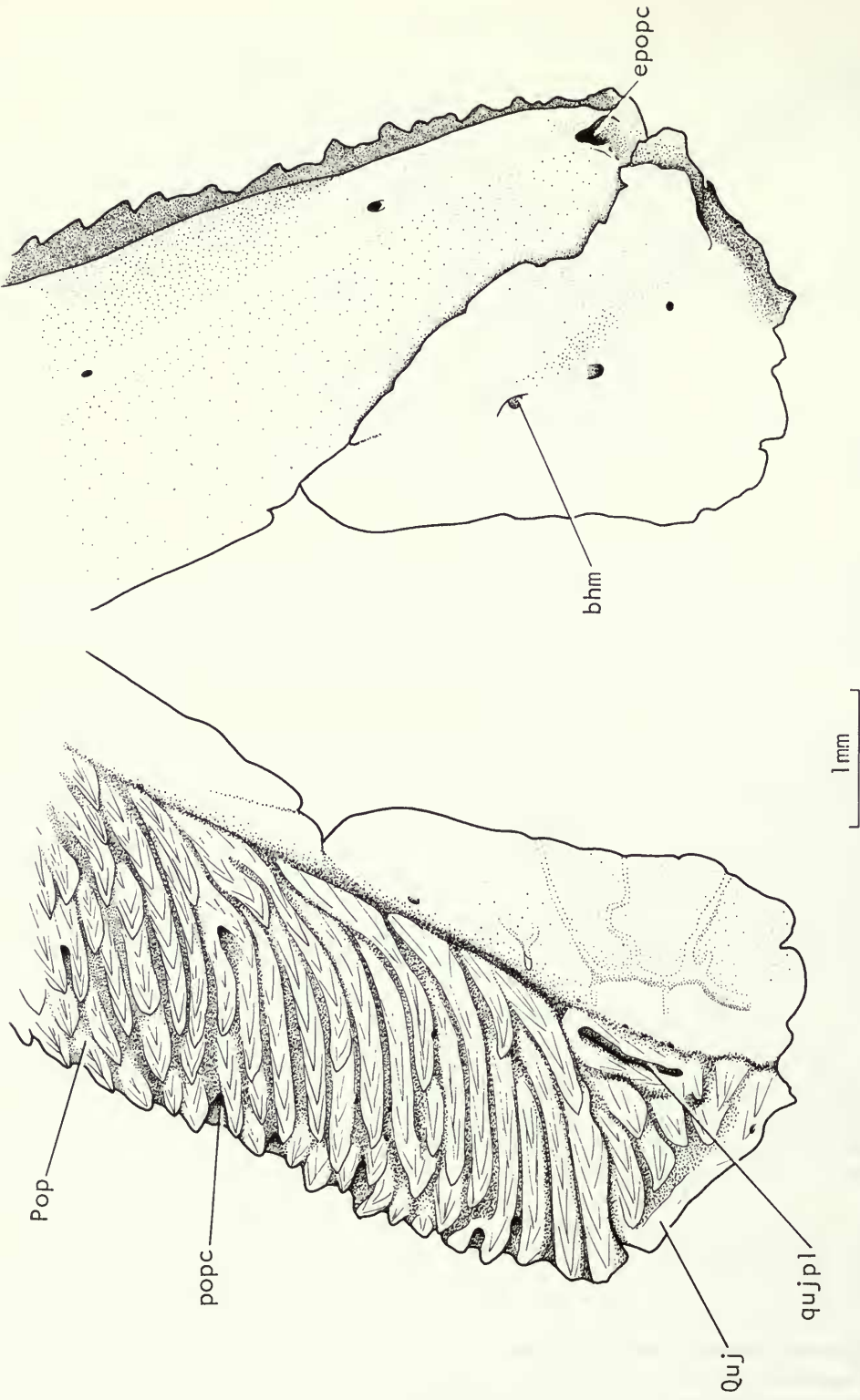


Fig. 64 *Moythomasia durgaringa* Gardiner & Bartram. Ventral end of right preopercular and quadratojugal in lateral (left) and medial views, from BMNH P.56502.

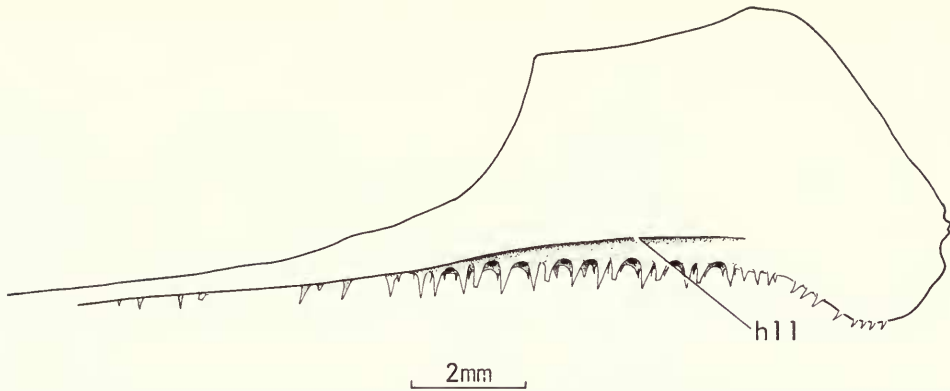


Fig. 65 *Mimia toombsi* Gardiner & Bartram. Right maxilla in medial view, from BMNH P.56486.

(intermediating body or symphyseal portion) then chondrifies to form the palatoquadrate commissure and is incorporated in the floor of the ethmoid region.

In *Amia*, *Lepisosteus* and teleosts (Holmgren 1943, Bertmar 1959) the primary palatoquadrate commissure chondrifies as a single unit which later fuses into the ethmoid plate. In *Acipenser* (Holmgren 1943: figs 26, 28) this primary commissure is possibly represented by the so-called tentacle blastemas.

In selachians (Holmgren 1940), although there is always an early, mesenchymatic, frontal connection between the palatoquadrates and the trabeculae, there is never an intermediating body or symphyseal portion joining the palatoquadrates to the floor of the ethmoid region. Instead, somewhat later in development, after the formation of the basal (orbital) processes, the anterior ends of the palatoquadrates grow forwards and inwards to meet in the mid-line, forming a symphysis (see under anterior articulation, p. 297) which ventrally supports teeth. This symphysis is found in all extant selachians. A similar shark-like palatoquadrate commissure is seen in *Acipenser* (where it must be considered to be secondary, not primitive; see below under anterior articulation), and in the acanthodian *Ptomacanthus* (Miles 1973b: pl. 6) and possibly in the placoderm *Jagorina* (Stensiö 1969: 71).

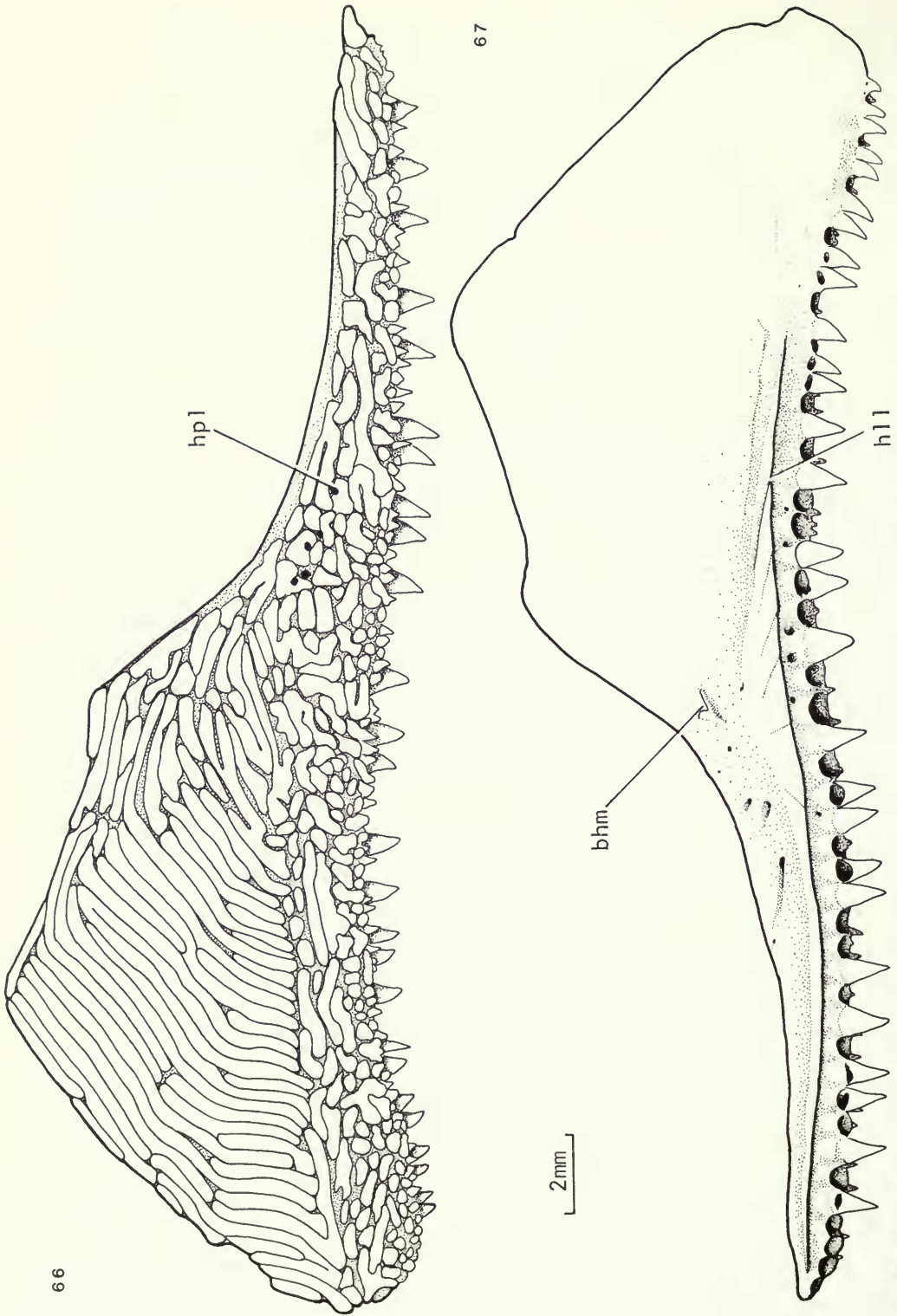
In osteichthyans the vomer develops beneath the primary palatoquadrate commissure and therefore lies in sequence with the dermopalatines. From this it follows that the dermopalatine-vomer sequence is homologous throughout the osteichthyans.

The vomer is paired in *Mimia*, *Moythomasia*, *Boreosomus*, saurichthyids (Gardiner 1960: fig. 21), '*Aspidorhynchus*', *Lepisosteus*, caturids (Gardiner 1960: fig. 36), parasemionotids (Patterson 1975: figs 30, 41), *Amia*, pachycormids (Lehman 1949: fig. 4; Patterson 1975: 513), and the teleosts *Hiodon* and *Osmerus* (Patterson 1975: 513).

There is a median vomer in living chondrosteans (toothless in *Polyodon*, *Acipenser* and *Scaphirhynchus*, Sewertzoff 1926: figs 3, 4, 39, the so-called median basirostral), *Bobasatrania* (Nielsen 1952: 199), in the semionotids *Dapedium* and *Lepidotes* (Gardiner 1960: 322), in pycnodonts, leptolepids and the majority of teleosts (Patterson 1975: 515). In the last group the vomer fuses with the ventral ethmoid during ontogeny. There is usually good evidence in teleostean embryology for the paired origin of the vomer (de Beer 1937: 126, 130, 159).

A vomer is absent in *Pteronisculus*, *Australosomus* and adult specimens of *Polypterus*. Nevertheless a binary primordium has been described in the 30 mm stage of *Polypterus bichir* by Holmgren & Stensiö (1936: 397), and a median vomer in the 24 mm, 32 mm and 125 mm stages of *Polypterus* by Pehrson (1947: 448).

The vomer is paired in actinistians (*Whiteia*, *Latimeria*, Millot & Anthony 1958), porolepids (*Porolepis*, *Glyptolepis*, *Holoptychius*, Jarvik 1972: pls 3, 17, 25) and osteolepids (*Megalichthys*, *Ectosteorhachis*, Jarvik 1966; *Eusthenopteron*, Jarvik 1942: fig. 56). In dipnoans it may be paired or median. The vomer is paired in *Uranolophus* (Denison 1968), *Dipnorhynchus* (anterior



Figs 66-67 *Moythomasia durgaringa* Gardiner & Bartram. Right maxilla, from BMNH P.53221. Fig. 66, lateral view. Fig. 67, medial view.

pterygoids of Thomson & Campbell 1971), *Griphognathus* (dermopalatinum of Schultze 1969: fig. 4; dermopalatine 1 of Miles 1977: fig. 57), *Ceratodus*, *Sagenodus*, *Uronemus* (Miles 1977: 175), *Conchopoma* (Schultze 1975), *Gnathorhiza* (Berman 1968), *Monongahela* (Lund 1970), *Neoceratodus*, *Lepidosiren* and *Protopterus* (Miles 1977: 175). There is a median vomer in *Chirodipterus*, *Holodipterus* (Miles 1977: figs 67, 87) and *Scaumenacia* (Jarvik 1967a: pl. 6).

The vomer is paired in Recent Amphibia, but median in Recent chelonians, lacertilians, birds and monotremes. However, in the development of these choanates with a median vomer there is often evidence of paired origin (de Beer 1937: 434).

In summary, the osteichthyan vomer is primitively a paired bone which fuses into a median element in actinopterygians, dipnoans, lacertilians, chelonians, birds and monotremes. In actinopterygians this fusion has occurred independently on at least five occasions, in *Polypterus*, in Recent chondrosteans, in *Bobasatrania*, in semionotids and pycnodonts, and in teleosts.

2. *Anterior articulation.* In actinopterygian ontogeny, after the separation of the intermediating body, the anterior ends of the palatoquadrates (the so-called pterygoid processes) come into close contact with the ethmoid region (postnasal wall). Subsequently an articulation develops between the anterior end of the palatoquadrate (autopalatine) and the lateral ethmoid, the rostro-palatine articulation. An anterior articulation is found in most actinopterygians, with the exception of Recent and fossil chondrosteans where in *Acipenser* and *Polyodon* the two palatoquadrate bars meet in the mid-line forming a symphysis well below the ethmoid region. In *Acipenser*, however, they are still connected with this region by a ligament (Holmgren 1943: fig. 27), much as in *Carcharhinus*. The palatoquadrates are separate and distinct in *Chondrosteus* (BMNH P.2048) and meet in the mid-line. The rostro-palatine articulation is single in primitive actinopterygians (*Mimia*, *Moythomasia*, *Polypterus*), *Amia* and halecomorphs, but in teleosts it is often double (*Salmo*, etc.; Gardiner 1973: 119).

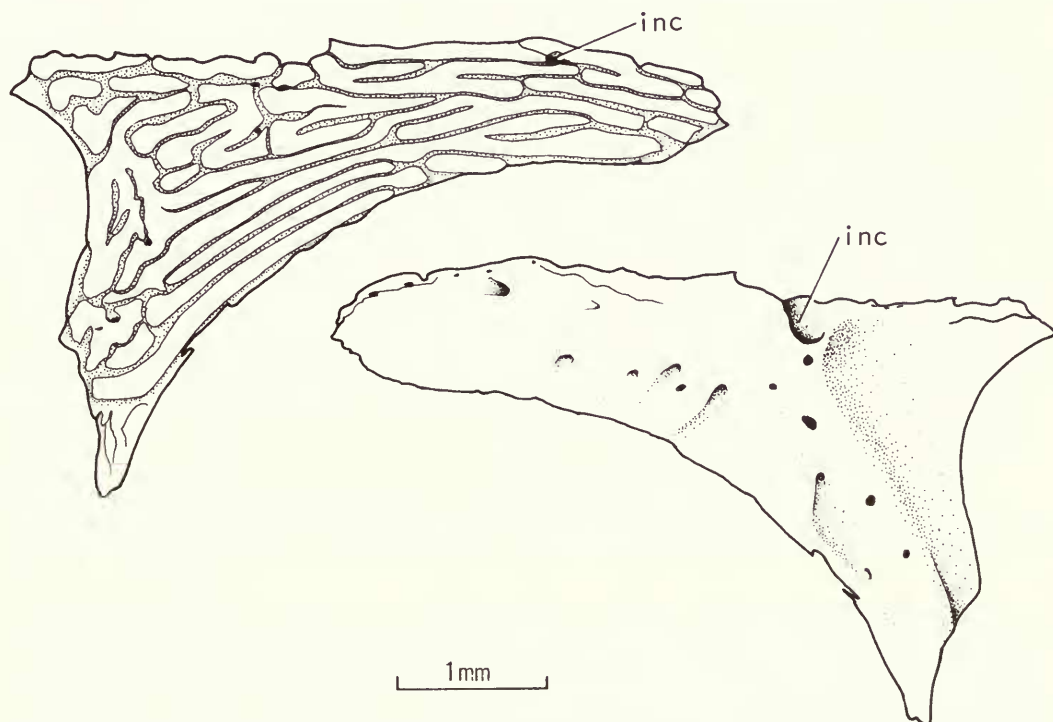


Fig. 68 *Mimia toombsi* Gardiner & Bartram. Right dermosphenotic in lateral (above) and medial views, from BMNH P.56483.

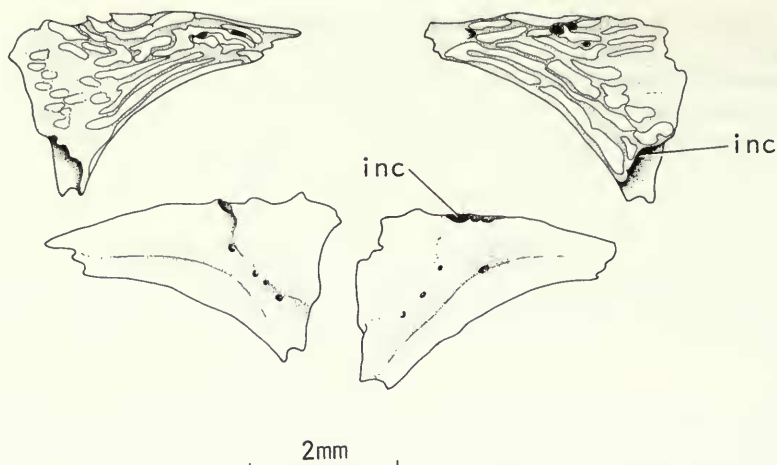


Fig. 69 *Moythomasia durgaringa* Gardiner & Bartram. Dermosphenotics in lateral (above) and medial views, from BMNH P.53255. The right dermosphenotic is on the left.

A similar, single rostro-palatine articulation is found in actinistians (*Latimeria*, *Rhabdoderma*, *Macropoma*, *Undina*), but in porolepids (*Glyptolepis* Jarvik 1972: fig. 25) and *Youngolepis* (Chang 1982) this articulation is supported by additional articulatory facets or points of fusion (Jarvik 1972: 71) between the autopalatine and suborbital shelf. In *Eusthenopteron* the rostro-palatine articulation is said to be double (Jarvik 1942: figs 48, 50, 54, art m, art l) but in an acid-prepared specimen (BMNH P.60310, Rosen *et al.* 1981) it is single. This articulation is supported by a more medial articulation between a dorsomedial process of the autopalatine and the orbital wall (suborbital shelf) (Jarvik 1954: figs 24, 40, pr.dm) and by the head of the dermopalatine which articulates with the vomer (Rosen *et al.* 1981: figs 13, 14). In *Polypterus* the primary rostro-palatine articulation is also supported by articulations of the dermopalatines.

In placoderms a single rostro-palatine articulation has been recorded in *Holonema* (Miles 1971b) and *Dicksonosteus* (Goujet 1975: fig. 4), and a double articulation in *Ctenurella* (Ørvig 1960: pl. 29, fig. 1; Miles & Young 1977: fig. 27D) and *Buchanosteus* (Young 1979: fig. 15). In acanthodians an anterior articulation is unknown and in the Permian *Acanthodes* (Miles 1965: fig. 1) the palatoquadrate extends forward only as far as the posterior rim of the orbit. Here there is no possibility of an anterior articulation (rostro-palatine), or of an anterior symphysis as in *Ptomacanthus* (Miles 1973b: pl. 6), because the palatine ossification has an unbroken covering of perichondral bone (Reis 1896). It cannot have had an unossified palatine process as proposed by Holmgren (1942: 138).

The palatoquadrate always meets its fellow in the mid-line in Recent selachians and may have a ligamentous attachment with the ethmoid region, as in *Carcharhinus*, or a sliding articulation, as in *Chlamydoselachus*.

On this evidence an anterior articulation cannot be primitive for gnathostomes. However, there is little doubt that a single anterior articulation is the primitive osteichthyan condition, with the autopalatine meeting the lateral ethmoid. The articulation of the autopalatine with the postnasal wall is considered synapomorphic for placoderms plus osteichthyans.

3. Otic process and palatobasal articulation. The posterodorsal expansion of the palatoquadrate is referred to as the otic process. This process is frequently single as in many chondrichthyans (*Cladoseleche*, *Cladodus*, *Xenacanthus*, *Squalus*, *Heterodontus*), placoderms (*Ctenurella*, *Buchanosteus*, Young 1979: figs 2, 12), acanthodians (*Climatius*, Miles 1973b: fig. 8), actinopterygians (*Polypterus*, *Polyodon*) and actinistians (*Rhabdoderma*, *Wimania*, *Latimeria*). The otic process may be notched for the maxillary and mandibular branches of the Vth nerve

(*Chlamydoselachus*, *Mustelus*, *Acanthodes*, *Amia*, *Eusthenopteron*, *Porolepis*). When notched the anterior division of the otic process is referred to either as the basal (orbital) process (selachians, actinopterygians) or as the ascending process (actinistians, rhipidistians). The single dorsal process of tetrapods is also referred to as the ascending process. The connection which develops between the anteroventral region of the otic process (so-called basal process) and the basipterygoid process is referred to as the palatobasal articulation.

The basipterygoid process is typically developed in osteichthyans, but it is also recognizable in many selachians where it forms part of the subocular shelf as in *Heptranchias*, and in *Squalus* (Jollie 1971) where it arises from the site of the polar cartilages.

In living actinopterygians the contact between the palatoquadrate and basipterygoid processes is only to be seen in *Lepisosteus* (Hammarberg 1937: fig. 9) and *Acipenser* (Holmgren 1943: 30). In the latter a distinct blastema joins the palatoquadrate with the trabecula (Holmgren 1943: figs 26, 27), and this later transforms into a ligament which according to Bugajew (1929) may chondrify. However, no such chondrification was observed by de Beer (1937: 91), Edgeworth (1935) or Holmgren (1943: fig. 27).

In *Polypterus* (Budgett 1901), *Amia* and *Salmo* (Holmgren 1943: 37, 40) the basipterygoid process is not developed. Nevertheless in the development of *Amia* and *Salmo* the palatoquadrate is connected with the trabecula by means of a thin membrane along its upper border. In *Pteroniscus* there is either a tongue-like process of the metapterygoid (in part supported by a corresponding tongue on the entopterygoid; Nielsen 1942: figs 34–37), which articulates with the basipterygoid process, or there is a hole in the metapterygoid at the base of the otic process (Lehman 1952: fig. 53), as in *Mimia*, *Moythomasia* and *Kentuckia* (Rayner 1951: fig. 3), through which the basipterygoid process presumably slid during lateral movements of the palatoquadrate. There is an articular fossa at the base of the otic process in *Boreosomus* (Nielsen 1942: fig. 70), while in *Australosomus* (Nielsen 1949: fig. 28) the anterior edge of the otic process is produced into a prominent, medially-directed process. The loss of the palatobasal articulation in *Polypterus*, *Amia* and teleosts may be directly correlated with the loss of the endochondral basipterygoid process in these fishes and in *Polypterus* with the articulation of the entopterygoid with the parasphenoid.

In Devonian actinistians (*Nesides*, *Diplocercides*) the basipterygoid process articulates with the inside of the metapterygoid near the base of the otic process, where there is a marked articular fossa (Bjerring 1977: fig. 28F), but as in later actinopterygians the basipterygoid process is missing in *Macropoma*, *Rhabdoderma* and *Latimeria*.

In the porolepid *Glyptolepis* (Jarvik 1972: 58) and in the osteolepids *Megalichthys* and *Eusthenopteron* (Jarvik 1954: figs 16, 22B) the condition is much as in *Nesides*, with a well-developed basipterygoid process articulating with the base of the otic process; the latter extends almost to the underside of the fronto-ethmoidal shield and there articulates with the neurocranium.

In later acanthodians such as *Acanthodes* (Miles 1965: 238) there is a distinct notch in the anterior margin of the otic process and the anterior process (basal process) articulated with the basipterygoid process. The only difference from the condition in osteichthyans is that the anterior process is ossified by the autopalatine and not the metapterygoid.

In ptyctodont placoderms the otic process has a grooved medial surface for a presumed articulation with a basipterygoid process. A palatobasal articulation has also been described at the base of the otic process in arthrodires (*Buchanosteus*, Young 1979: figs 2, 12).

In dipnoans the base of the otic process fuses with the trabecula (de Beer 1937: 172) and its top fuses with the orbital wall during development. A similar fusion occurs in holocephalans, anurans and urodeles.

In the fossil amphibian *Palaeoherpeton* the otic process is prominent and is ossified by the epipterygoid. Ventrally on its inner surface there is a distinct roughened recess (Panchen 1964: fig. 5), where it was probably in cartilaginous (immovable) contact with the basipterygoid process. In monotremes the otic process is ossified by the alisphenoid (Presley & Steel 1976) and consequently this bone may be homologous with the osteichthyan metapterygoid and the amphibian and 'reptilian' epipterygoid (Broom 1914).

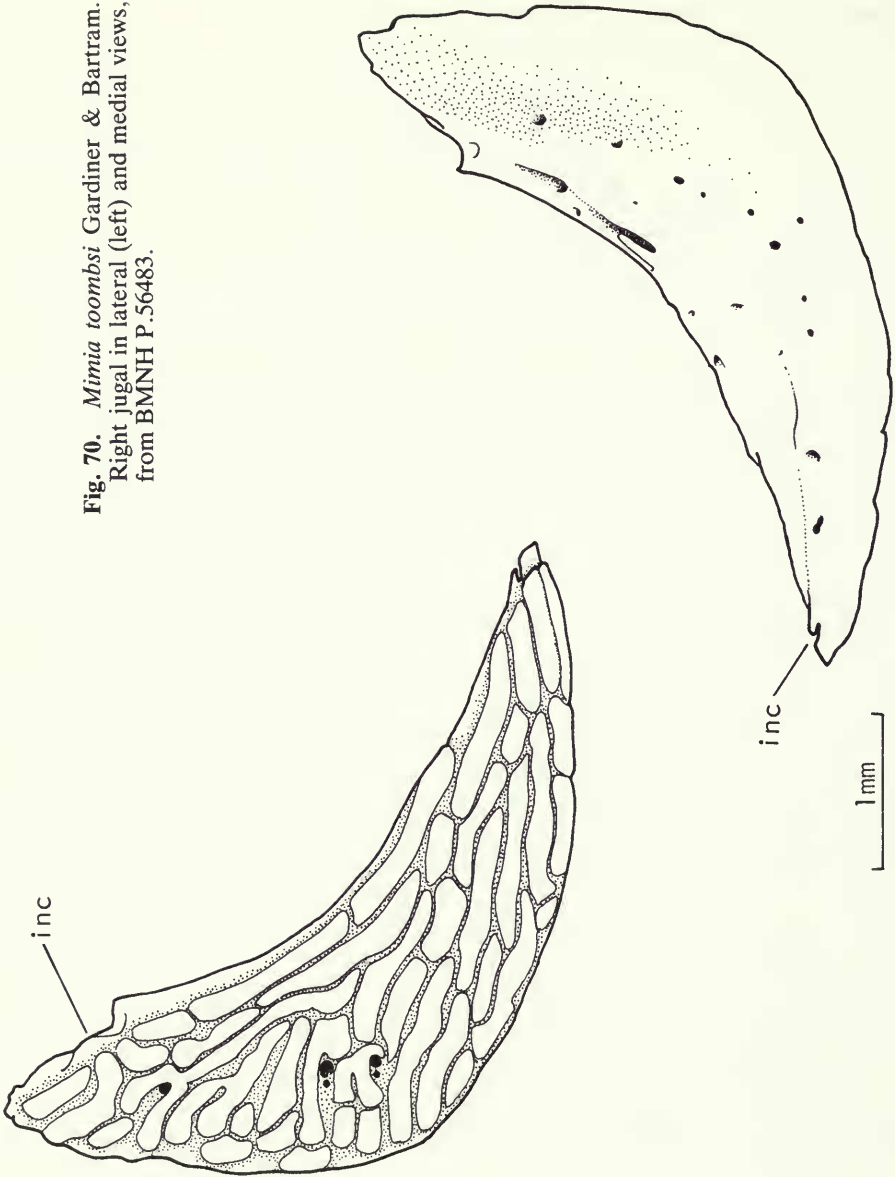


Fig. 70. *Mimia toombsi* Gardiner & Bartram.
Right jugal in lateral (left) and medial views,
from BMNH P.56483.

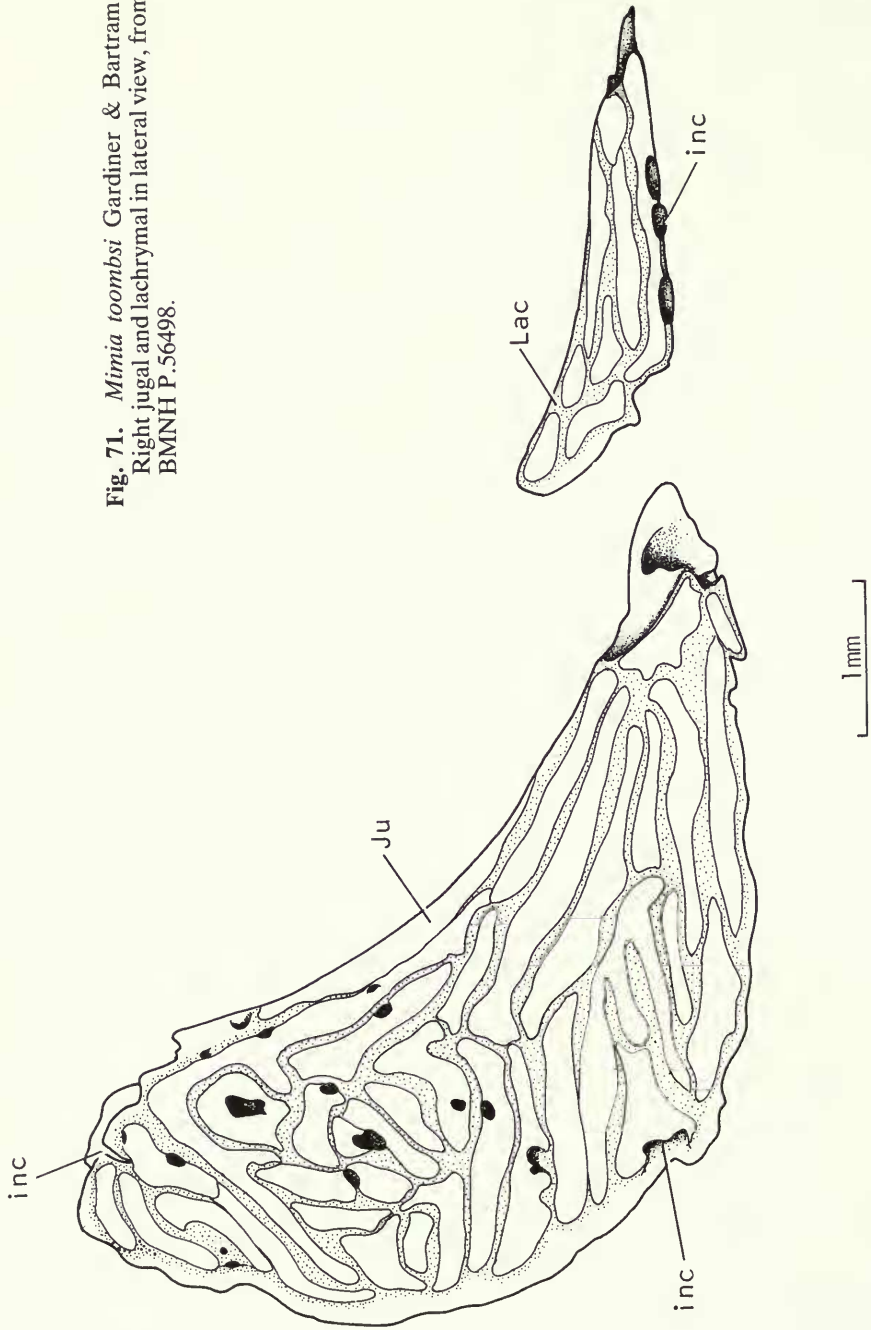
The palatoquadrate and Meckel's cartilages are generally regarded as the epimandibular and ceratomandibular elements respectively, with the anterior division of the otic process (basal process) often being regarded as dorsalmost elements of a branchial arch (Huxley 1876; de Beer 1937). Sewertzoff & Disler (1924) suggested that the basal process (anterior otic process) is serially homologous with the pharyngobranchials of the succeeding visceral arches; Holmgren (1943: 64) and Bertmar (1959) homologized it with the actinopterygian suprapharyngobranchial. The evidence for considering the anterior division of the otic process a pharyngomandibular rests on the claims of Sewertzoff & Disler (1924) that there is an independent nodule of cartilage (or prochondral rudiment) which fuses to the medial surface of the basal process in *Squalus*, *Scyllium*, *Mustelus* and *Somniosus*, and on the presence of separate cartilages in the anterior region of the palatoquadrate in *Scaphirhynchus* and *Acipenser* (Bugajew 1929). However, de Beer found no evidence of this cartilage in any of his specimens of *Squalus* (1937: pls 11, 12) or *Scyllium* (1937: pls 13, 14, 15), nor did Holmgren (1940) find any trace of a separate nodule in his exhaustive study of the embryology of *Squalus* and *Etmopterus*. Holmgren concluded (1943: 64) that 'in Squaloid sharks the orbital process is formed in continuum with the palatoquadrate proper'. Nevertheless he found that in *Scyllium* (Holmgren 1940: 153; fig. 104) and *Mustelus* (1943: 53) the anterior division of the otic process (basal process) had a separate blastemic origin, although it subsequently chondrified in conjunction with the remainder of the palatoquadrate (1940: 164). The cartilages described by Ivanzoff (1887) in *Scaphirhynchus* and by Bugajew (1929: 98) in *Acipenser* lie in the connective tissue covering the basitrabecular process and thus do not appear to belong to the palatoquadrate. There is therefore no evidence in the development of the anterior division of the otic process (basal process) to support the theory that it is a pharyngomandibular. Moreover since suprapharyngobranchials appear to be an osteichthyan specialization (see p. 362) there is even less evidence for considering the anterior otic process to be a suprapharyngomandibular.

Unfortunately the situation is further complicated by the assumption of several workers (Holmgren 1943) that the anterior division of the otic process of actinopterygians is not homologous with the selachian anterior otic process and that neither is homologous with the choanate otic (ascending) process (Goodrich 1930: 413; de Beer 1937: 419). But the so-called ascending process which is presumed by Goodrich (1930: 413) and de Beer (1937: 420) to be present only in Dipnoi and tetrapods is no more than a dorsally extended otic process, much as in *Nesides* (Jarvik 1954: fig. 15), *Glyptolepis* (Jarvik 1972: fig. 25) and *Eusthenopteron* (Jarvik 1954: fig. 23B). In actinistians, porolepids and *Eusthenopteron* the top edge of the otic process articulates with the postorbital process (antotic process). In dipnoans and Recent amphibians the top of the process fuses with the neurocranium (orbital cartilage). From these comparisons it follows that both the single otic process and the palatobasal articulation may be regarded as primitive gnathosome characters. The palatoquadrates of *Ctenurella* and *Jagorina* suggest that the omega-shaped (Schaeffer 1975) palatoquadrates of other placoderms are derived.

4. *Otic process and prespiracular cartilage.* In both fossil and Recent selachians the otic process is prominent and in '*Cladodus*', *Xenacanthus*, *Tamiobatis* (Romer 1964), *Hybodus* (Maisey 1982, 1983), *Heptranchias* (Daniel 1934) and *Pseudocarcharias* (Compagno 1973: 20) it articulates with the postorbital process as in *Acanthodes*. In the majority of sharks the process does not articulate with the braincase (e.g., *Chlamydoselachus*, *Etmopterus*, *Isurus*, *Oxyrinotus*, *Scyliorhinus*, *Squalus*), and the otic process is missing in rays (e.g., *Raja*) and in *Urolophus* (Holmgren 1940: fig. 181).

Both de Beer (1937: 420) and Holmgren (1943: 61) believed that in many selachians (*Scyllium*, *Squalus*, etc.), the otic process becomes detached as the prespiracular cartilage (or spiracular rudiment). In the development of *Heterodontus*, *Raja*, *Urolophus* and *Etmopterus* Holmgren (1940; 1943: 60) has shown how the spiracular rudiment arises as a mesenchymatic lamella, partly attached to the margin of the palatoquadrate anterior to the spiracular canal. It subsequently contacts the postorbital process and fuses with it dorsally. Later that part of the rudiment in front of the spiracle chondrifies independently of the palatoquadrate, with which it loses contact, as the prespiracular cartilage. In *Etmopterus* Holmgren (1940: fig. 95) described

Fig. 71. *Mimia toombsi* Gardiner & Bartram.
Right jugal and lachrymal in lateral view, from
BMNH P.56498.



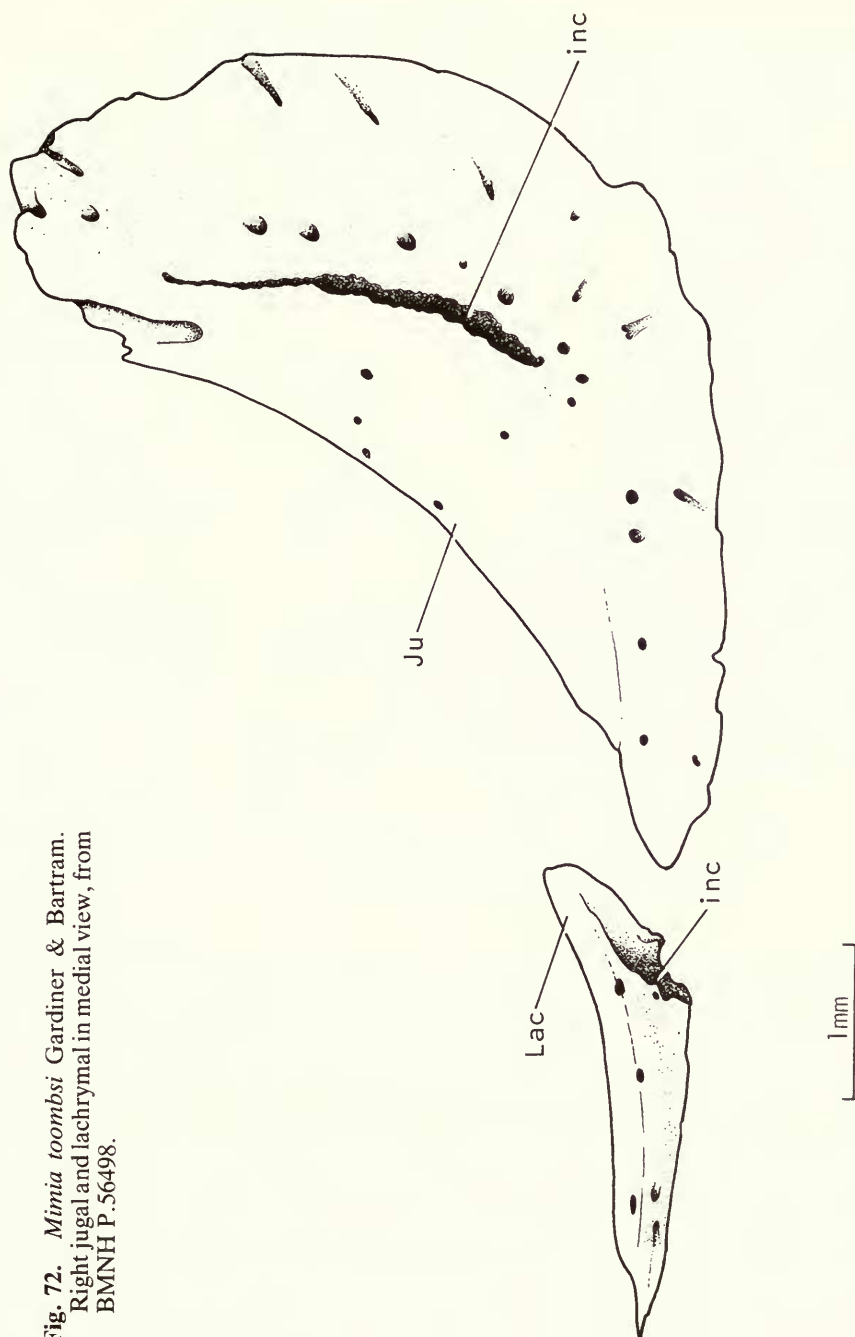


Fig. 72. *Mimia toombsi* Gardiner & Bartram.
Right jugal and lachrymal in medial view, from
BMNH P.56498.

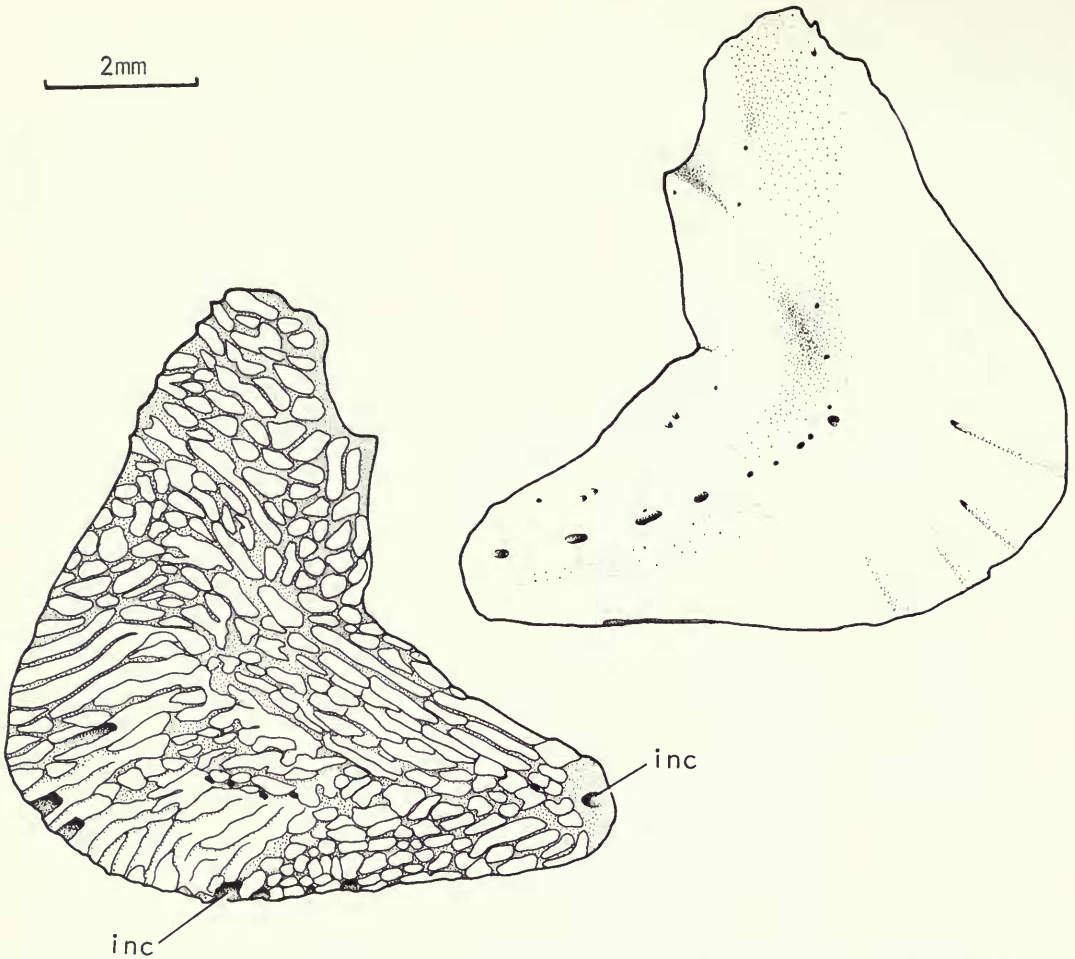


Fig. 73 *Moythomasia durgaringa* Gardiner & Bartram. Right jugal in lateral (left) and medial views, from BMNH P.53221.

both an otic process and a prespiracular cartilage and it became increasingly difficult to see how the prespiracular cartilage could be the homologue of the otic process. In order to resolve this apparent dilemma, Holmgren (1940: 140, 144; 1943: 56, 62) suggested that in *Etmopterus* the otic process was not homologous with that in some other selachians (notidanids), dipnoans and amphibians and that there were two distinct otic processes in sharks and rays, the processus oticus externus and the processus oticus internus. He showed that the processus oticus externus (1940: 140; 1943: 62) developed from the fusion of an extra palatoquadrate blastema with the palatoquadrate blastema, after which chondrification took place, while the processus oticus internus (1940: 131; 1943: 62) formed simultaneously as the lateral commissure. In 1940 Holmgren concluded that the otic process in *Etmopterus* was homologous with that in *Heptatranchias*, but in 1943 he was so confused that he at first considered them not the same, then homologous and finally non-homologous all on the same page (p. 62). It is very difficult to comprehend the movements and fusions of the various cell masses associated with the development of the palatoquadrate in selachians as described by Holmgren (1940, 1943), but if we confine our attention to the cartilage it is remarkably similar to that in osteichthyans. Further, since the palatoquadrate and prespiracular cartilages always chondrify as separate structures there is no reason to believe the latter to be a detached otic process, especially when

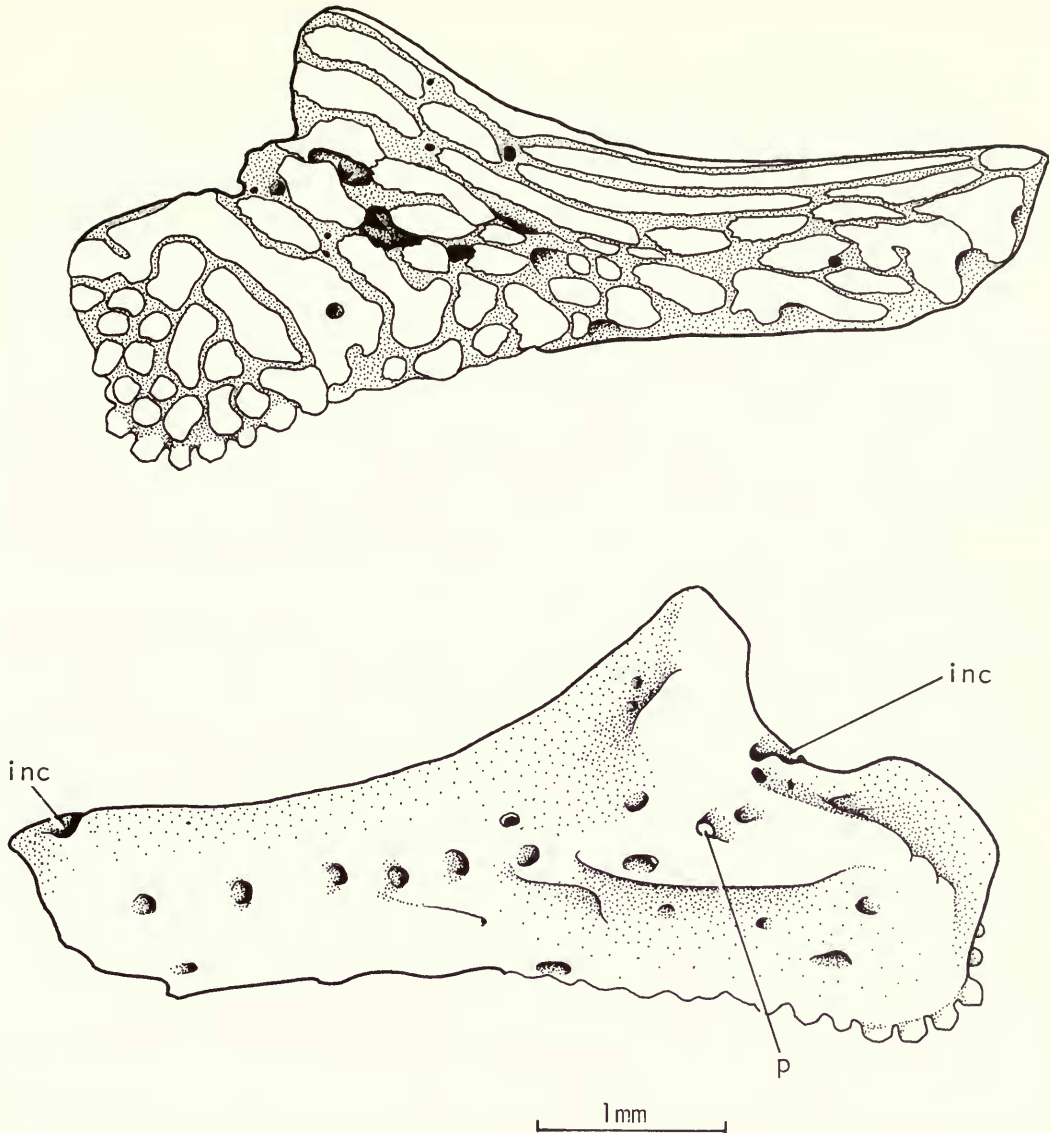


Fig. 74 *Moythomasia durgaringa* Gardiner & Bartram. Left lachrymal in lateral (above) and medial views, from BMNH P.53221.

both an otic process and a prespiracular cartilage are to be found in *Etmopterus* and *Chlamydoselachus*. There is even less evidence to support the view that the lateral commissure is yet another detached otic process, since a lateral commissure also occurs in *Etmopterus*.

5. Ossifications of the palatoquadrate. (a) **CARTILAGE BONES.** In primitive actinopterygians such as *Mimia*, *Moythomasia*, *Polypterus* (Allis 1922: 244), *Pteronisculus* (Nielsen 1942: 143) and *Acropholis* (Aldinger 1937: 43) the palatoquadrate ossifies from three centres, the autopalatine, metapterygoid and quadrate. Conditions are similar in more advanced forms such as *Amia*, *Pholidophorus* and teleosts (e.g. *Salmo*, *Gasterosteus*, *Cyclopterus*, de Beer 1937). However, in *Lepisosteus*, *Macromesodon* (Nursall 1966) and some teleosts there is no autopalatine (Patterson 1973: 246). In larger specimens of *Mimia*, *Moythomasia*, *Pteronisculus*, other

palaeoniscids (*Elonichthys*, *Boreolepis*, Aldinger 1937: 126) and *Ospia* (Stensiö 1932b: 252) fusion of individual bones during ontogeny must have occurred because the palatoquadrate is ossified throughout as one bone. In other specimens of *Pteronisculus* (Nielsen 1942: 143), *Saurichthys* (Stensiö 1925: 97), *Acropholis* (Aldinger 1937: 43) and *Boreosomus* (Stensiö 1921: 211) there are only two ossifications. Actinistians have the same three ossifications as actinopterygians (*Nesides*, Jarvik 1954: fig. 15; *Macropoma*, *Undina*, *Rhabdoderma*, Forey 1981: fig. 4; *Latimeria*, Millot & Anthony 1958) and this is undoubtedly the primitive osteichthyan condition.

In all described porolepids (Jarvik 1972: 72) and in *Eusthenopteron* (Jarvik 1954: fig. 16) the palatoquadrate shows no signs of subdivision, but is a single ossification, as in larger specimens of *Mimia* and *Pteronisculus*. In *Megalichthys* Watson (1926: 247; fig. 33) described a continuous series of endochondral suprapterygoid bones, but as in his descriptions of palaeoniscid palates Watson (1925: 852; 1928: 52) misinterpreted the material. In his figured specimen of *Megalichthys* the epipterygoid, suprapterygoids and quadrate are all one ossification. In the palaeoniscids *Elonichthys pectinatus* (Watson 1925: 852; fig. 21), *Elonichthys binneyi* (Watson 1925: fig. 22) and *Elonichthys aitkeni* (Watson 1925: fig. 23) the so-called suprapterygoids are all dermal bones (see under dermometapterygoid, p. 310), but in *Nematoptychius greenocki* (Watson 1925: fig. 26; 1928) and *Gonatodus* (Watson 1925: fig. 27) the anterior suprapterygoid is part of the autopalatine and the posterior suprapterygoid is part of the dermometapterygoid. Thus there is no evidence of more than three ossifications in the palatoquadrate of osteichthyans.

The palatoquadrate in Dipnoi is attached to the auditory capsule and to the orbitotemporal region of the neurocranium by the otic and antorbital processes (Sewertzoff 1902: 593), and in Recent forms its only ossification is the quadrate in *Neoceratodus*.

The palatoquadrate in fossil dipnoans is large, rigidly fused to the neurocranium, and ossified throughout as one bone. From its size and complexity in *Dipnorhynchus* (Thomson & Campbell 1971: fig. 27), *Griphognathus*, *Holodipterus*, *Chirodipterus* (Miles 1977: figs 14, 22, 35, 53) and *Stomiahykus* (Bernacsek 1977: fig. 8) it is difficult to believe that it is ossified entirely by the quadrate and it is likely that at least a metapterygoid was also present in its ontogeny.

In urodeles and apodans (*Triton*, *Cryptobranchus*, *Ichthyophis*) only the quadrate ossifies in the palatoquadrate, as in *Neoceratodus*. But in fossil amphibians such as *Palaeoherpeton* there is both a quadrate and a metapterygoid (the epipterygoid of Watson, 1926). Similarly in lacertilians, chelonians and *Sphenodon* both quadrate and metapterygoid (epipterygoid) are present.

In *Acanthodes* (Miles 1965: fig. 1) three perichondral ossifications exist in the palatoquadrate cartilage, a large quadrate, smaller metapterygoid and much smaller autopalatine. The quadrate and metapterygoid are separated by a large unossified portion, much as in smaller specimens of *Pteronisculus* (Nielsen 1942: 143).

In arthrodiran placoderms the palatoquadrate sometimes contains two perichondral ossifications, an anterior autopalatine and a posterior quadrate which is fused to the inner surface of the postsuborbital (Miles 1971b: figs 8, 9B). The two ossifications are separated by a large unossified area as in *Acanthodes* and some specimens of *Pteronisculus*. In *Dicksonosteus* (Goujet 1975: fig. 2) the palatoquadrate is perichondrally ossified as one bone, as it is in *Jagorina* (Stensiö 1969). In the ptactodont *Ctenurella* (Ørvig 1960, 1962) the palatoquadrate is perichondrally ossified in three separate ossifications, autopalatine, metapterygoid and quadrate, which are of approximately the same size (Miles & Young 1977: fig. 23).

Three ossifications in the palatoquadrate cartilage must be the primitive osteichthyan condition, considered synapomorphous for a group containing acanthodians, placoderms and osteichthyans.

(b) DERMAL BONES. Lining the roof of the mouth of osteichthyans is an extensive sheet of tooth-bearing dermal bones associated with the oral face of the palatoquadrate. In actinopterygians these bones form two series: an outer or ventral arcade comprising the ectopterygoid and dermopalatines and an inner or dorsal series which primitively included

dermometapterygoids and an entopterygoid (Fig. 75A, B). In all other osteichthyans the inner or dorsal series (dermometapterygoids and entopterygoid) is absent (Figs 75C, D, 76).

As Rosen *et al.* (1981) suggest, cladistic relationships of sarcopterygians require reduction rather than increase in palatal bones. Thus the presence of dermometapterygoid and entopterygoid bones is regarded as primitive rather than a synapomorphy of actinopterygians.

(c) ECTOPTERYGOID. Embryologically the ectopterygoid forms in sequence with the dermopalatines in *Polypterus* (Pehrson 1947: fig. 28), *Amia* (Pehrson 1922) and many teleosts (*Salmo*, *Clupea*, etc.). In juvenile specimens of *Mimia* (Figs 53, 54), *Pteronisculus*, *Boreosomus* (Nielsen 1942: figs 34, 71), *Birgeria* (Nielsen 1949: fig. 71) and *Elonichthys* (Watson 1925: fig. 21), the ectopterygoid and dermopalatine clearly belong to the same series.

Primitively the ectopterygoid covers the posteroventral part of the oral face of the palatoquadrate and overlies that part of the palatoquadrate which bounds the adductor opening (*Pteronisculus*, *Boreosomus*, *Birgeria*, *Elonichthys*, *Mimia*, *Polypterus*). It also joins the maxilla anteroventrally and the quadrate posteriorly (*Mimia*, Fig. 56; *Pteronisculus*, *Boreosomus*, Nielsen 1942: 151; fig. 71; *Australosomus*, *Birgeria*, Nielsen 1949: figs 26, 71; *Elonichthys*, Watson 1925: fig. 22; *Polypterus*, Allis 1922: fig. 25). Further, the centre of ossification of the ectopterygoid is on a level with the most anterior part of the adductor opening, just where the ectopterygoid meets the maxilla (*Pteronisculus*, Nielsen 1942: fig. 37; *Australosomus*, *Birgeria*, Nielsen 1949: 105, 232; *Mimia*, Fig. 53; *Polypterus*, Pehrson 1947: fig. 28).

Since the ectopterygoid of actinopterygians reaches back to the quadrate and is the posterior member of a series with the dermopalatines, it is clear that this bone is not homologous with the bone called the ectopterygoid in actinistians (*Macropoma*, Watson 1921: fig. 4, ecpt), porolepids (*Glyptolepis*, Jarvik 1972: fig. 31, Ecpt), osteolepids (*Eusthenopteron*, Jarvik 1954: fig. 16, Ecpt) and tetrapods (Presley & Steel 1978: fig. 2, ect). The ectopterygoid of non-actinopterygians compares more favourably with the actinopterygian dermopalatine (see below). On positional and other anatomical and developmental evidence the actinopterygian ectopterygoid is better homologized with the entopterygoid of actinistians, lungfishes and the pterygoid of tetrapods (Figs 75, 76).

(d) DERMOPALATINES. The dermopalatines form a series of interdigitating bones associated with the anteroventral region of the palatoquadrate. Within the palaeoniscids a varying number of dermopalatines has been recorded: four in *Watsonichthys* (Watson 1925: fig. 21, pal.1-4), three or four in *Mimia* (Figs 53, 54), three in *Mesonichthys* (Watson 1925: fig. 23), two in *Elonichthys* (Watson 1925: fig. 22), *Nematoptychius* (Watson 1925: fig. 26), *Pteronisculus*, *Boreosomus* and *Birgeria* (Nielsen 1942: figs 34, 71; 1949: fig. 71). There is one in *Gonatodus* (Watson 1925: fig. 27), *Namaichthys* (Gardiner 1962: fig. 3) and *Polypterus*. In *Amia* there are two dermopalatines, but in most higher actinopterygians there is only one (*Lepidotes*, Gardiner 1960: fig. 47; *Lepisosteus*; *Ospia*; *Elops*, Nybelin 1968: fig. 1). In many teleosts (e.g. *Salmo*, de Beer 1937: 126) this single dermopalatine fuses with the autopalatine to form a composite bone. Dermopalatines are missing in *Australosomus* (Nielsen 1949: fig. 30) and pycnodonts (*Macromesodon*, Nursall 1966). In actinistians the so-called ectopterygoid (Millot & Anthony 1958) is undoubtedly a member of the dermopalatine series; in many fossil forms the corresponding bone is indistinguishable in size and shape from the preceding dermopalatine with which it is closely sutured (e.g. *Macropoma*, P. L. Forey, personal communication). Thus the ectopterygoid of actinistians is better regarded as a posterior dermopalatine, in which case all actinistians possess three dermopalatines as in *Mimia* and *Watsonichthys*.

In porolepids (*Glyptolepis*, Jarvik 1972: fig. 31) the ectopterygoid is again in sequence with an anterior dermopalatine which it resembles in shape, size and disposition of teeth; and similarly in the osteolepids *Eusthenopteron* (Jarvik 1954: fig. 16) and *Glyptopoma* (Jarvik 1950: fig. 6).

Thus in porolepids, osteolepids and onychodonts (Andrews 1973: 146) there are always two dermopalatines (not three as in actinistians), and in this respect these fishes resemble *Amia* and tetrapods. Primitively in tetrapods there are two palatines, an anterior dermopalatine and a more posterior transpalatine (ectopterygoid of Presley & Steel 1978) and their homology with the two dermopalatines in porolepids and osteolepids can be established by positional evidence.

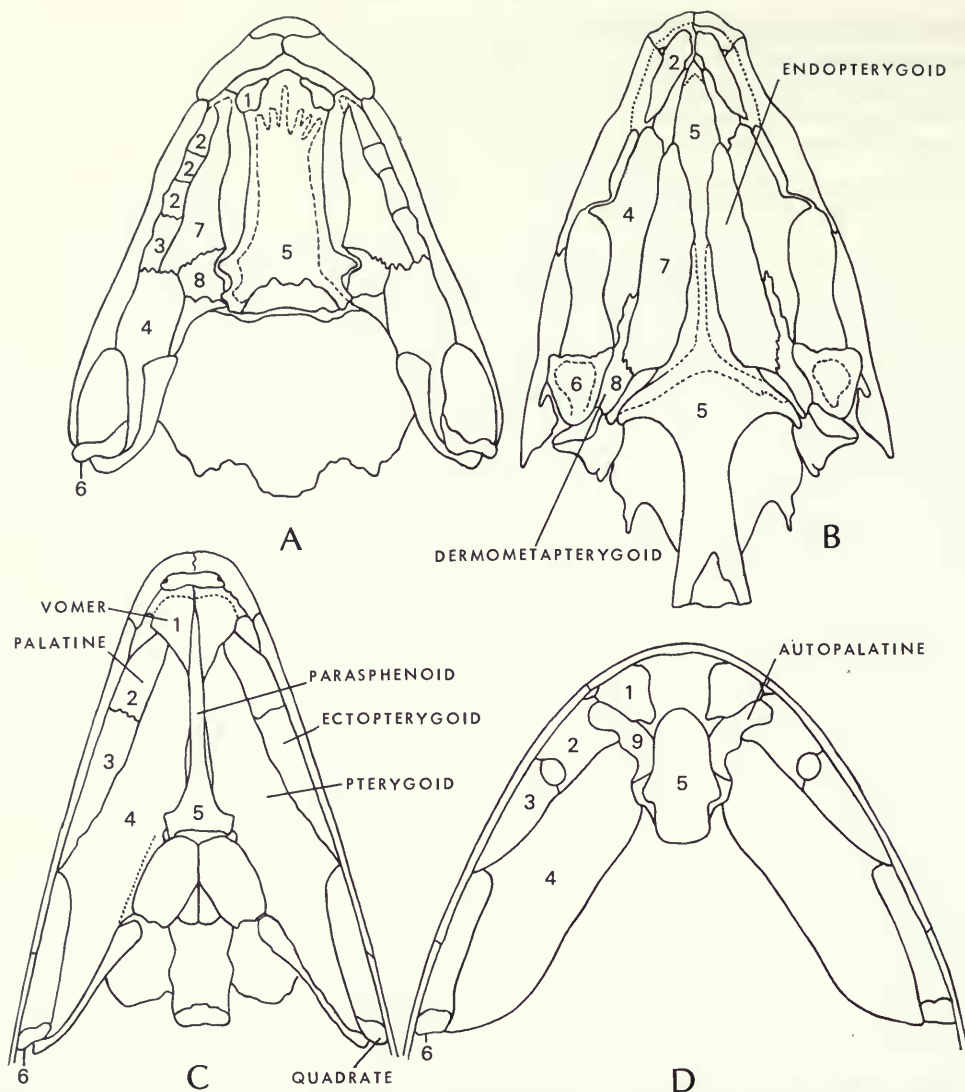


Fig. 75 Palates in ventral view and suggested homology of dermal bones and their relation to palatoquadrate. A, *Mimia toombsi* Gardiner & Bartram; B, *Polypterus bichir* Saint-Hilaire; C, *Eusthenopteron foordi* Whiteaves (from Jarvik 1954); D, *Glyptolepis groenlandica* Jarvik (from Jarvik 1972). Compare Fig. 76. From Rosen *et al.* (1981).

In Recent dipnoans both dermopalatine and ectopterygoid are missing but in the fossil *Griphognathus* (Miles 1977: fig. 57, Dpl₂) one bone of this series remains, which from its position bordering the medial edge of the fenestra ex oculo, must be homologous with the dermopalatine of tetrapods. A similar parallel loss of the transpalatine has occurred in the Lissamphibia; in the urodeles *Salamandra* and *Cryptobranchus* the palatine also disappears at metamorphosis (Wintrebert 1922: 239). The transpalatine is also missing in chelonians and several fossil 'reptiles' (*Placodus*, *Ichthyosaurus*, etc).

(c) ENTOPTERYGOID. The entopterygoid is a single ossification¹ which occurs in almost all

¹Re-examination of the specimen of *Cheirolepis* (BMNH P.36061) described by Pearson & Westoll (1979: fig. 8) has convinced me that what they call lines of individual entopterygoids are no more than fragments of a broken dermal cheek bone.

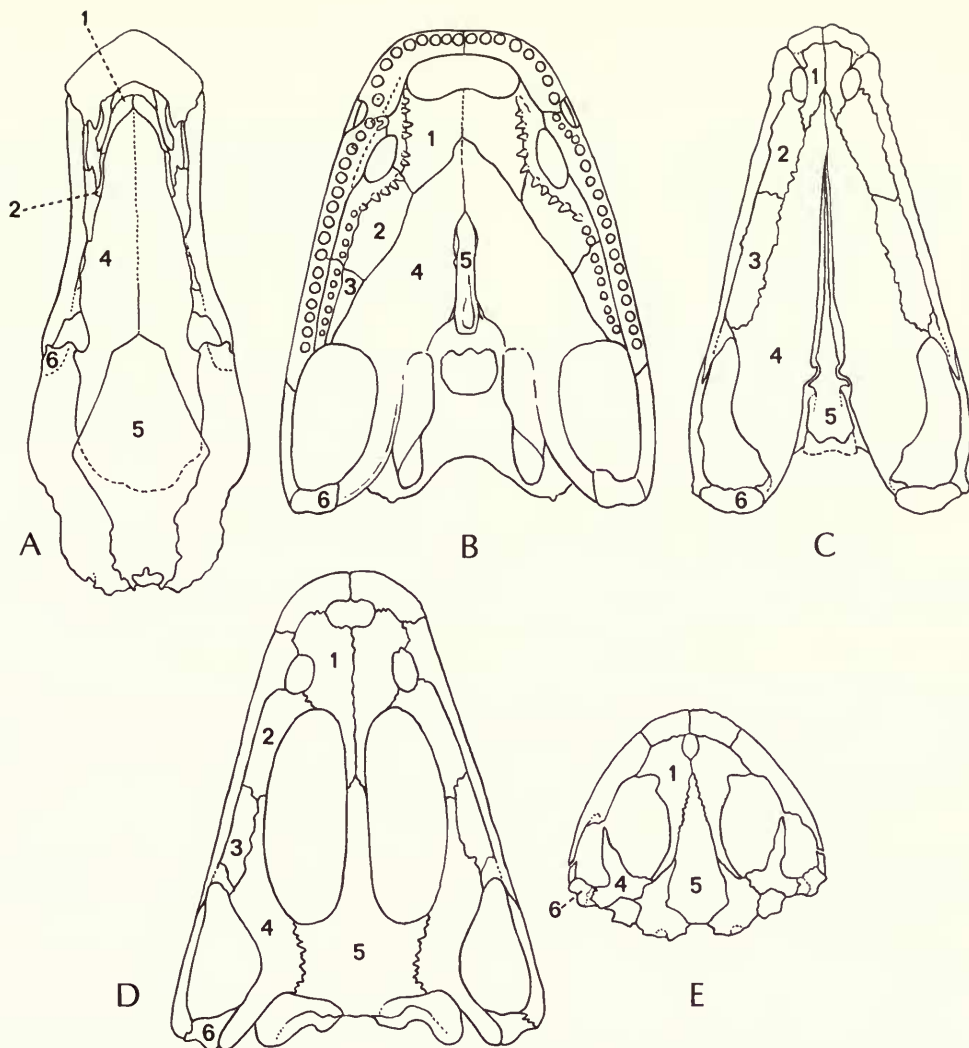


Fig. 76 Palates in ventral view and suggested homology of dermal bones and their relation to palatoquadrate. A, *Griphognathus whitei* Miles (from Miles 1977); B, *Ichthyostega* sp. (from Romer 1966); C, *Eogyrinus attheyi* Watson (from Panchen 1972); D, *Benthosuchus sushkini* Efremov (from Bystrov & Efremov 1940); E, *Tylotriton verrucosus* Riese (from Noble 1931). Compare Fig. 75. From Rosen *et al.* (1981).

actinopterygians with the exception of pycnodonts (*Macromesodon*, Nursall 1966). It is not found in any other osteichthyan. In *Polypterus* the entopterygoid arises in series with the dermometapterygoid (Pehrson 1947: 448), somewhat later in ontogeny than the ectopterygoid and dermopalatine. Although in *Mimia* (Enpt, Figs 53, 54) the entopterygoid could be regarded as being in series with either the ectopterygoid or dermometapterygoids, in most palaeoniscids (and *Polypterus*) it is clearly in series with the dermometapterygoid. Further, in *Pteronisculus* (Nielsen 1942: fig. 37) and *Polypterus* the centres of ossification of the entopterygoid and dermometapterygoid lie near the middle of the dorsal margin of those bones whereas the centres of ossification of the ectopterygoid and dermopalatines are at or near their ventral margins. The centre of ossification of the entopterygoid in *Mimia* also lies near its dorsal margin and similarly in *Amia* and *Elops*.

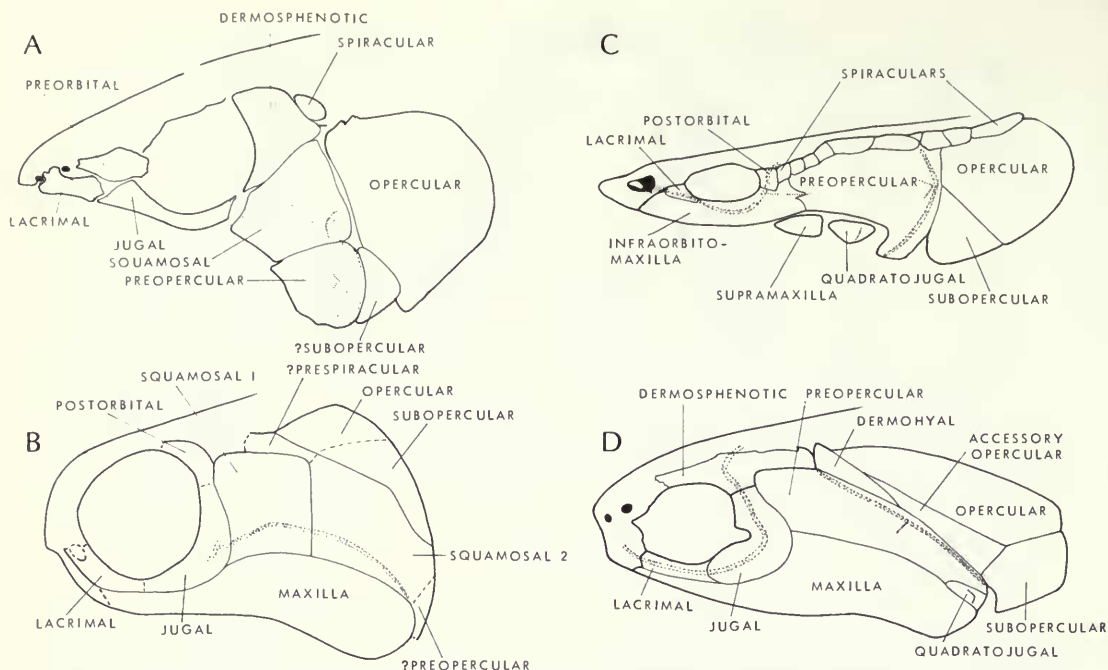


Fig. 77 Cheek bones and operculum. A, *Rhabdoderma elegans* (Newberry) (after Forey 1981); B, *Strunius walteri* Jessen (after Jessen 1966); C, *Polypterus bichir* Saint-Hilaire (after Daget 1950); D, *Cheirolepis trailli* Agassiz (after Pearson & Westoll 1979). Bone names are those used by the authors cited. From Rosen *et al.* (1981).

The entopterygoid is primitively excluded from the jaw margin by the ectopterygoid and dermopalatines, but in *Australosomus* (Nielsen 1949: fig. 30), where the dermopalatines are absent, the entopterygoid contacts the maxilla anteriorly.

(f) **DERMOMETAPTERYGOID.** The dermometapterygoids form a series of interdigitating bones associated with the posterodorsal region of the palatoquadrate, in particular the metapterygoid. *Polypterus* and *Amia* are the only living fish with a dermometapterygoid. Within the palaeoniscids a varying number of dermometapterygoids have been recorded. There are five dermometapterygoids in *Watsonichthys* (Watson 1925: fig. 21, spt) and *Elonichthys binneyi* (Watson 1925: fig. 22, spt 2–6), four in *Mimia* (Dmpt, Figs 53, 54) and *Elonichthys aitkeni* (Watson 1925: fig. 23, the four small bones behind the accessory vomer, spt 1), and one in *Elonichthys caudalis*, *Elonichthys semistriatus*, *Gonatodus*, *Nematoptychius* (Watson 1925: figs 24, 25, 27, metpt; 1928: fig. 7), *Pteronisculus* (Nielsen 1942: fig. 37), *Birgeria* (Nielsen 1949: fig. 71), *Polypterus* and *Amia*. Both entopterygoid and dermometapterygoid bones are primitively present in actinopterygians but neither occurs in other osteichthyans.

We may also conclude that the primitive osteichthyan possessed a further row of tooth-bearing dermal bones consisting of a pterygoid (=ectopterygoid) and several dermopalatines (at least two).

Dermal bones of the cheek: summary and discussion

The bones of the cheek are fairly uniform throughout the osteichthyans (Figs 77, 78). Perhaps the one exception is the osteichthyan dermosphenotic (=postorbital of tetrapods). The dermosphenotic carries the infraorbital canal; it is lateral to the intertemporal in primitive actinopterygians and ventral to the so-called 'dermosphenotic' (Jarvik 1954, 1972) in osteolepids, and is in sequence with the infraorbital bones (jugal and lachrymal). It also forms the dorsolateral border to the spiracle in *Mimia*, *Moythomasia* and the spiracular pouch in

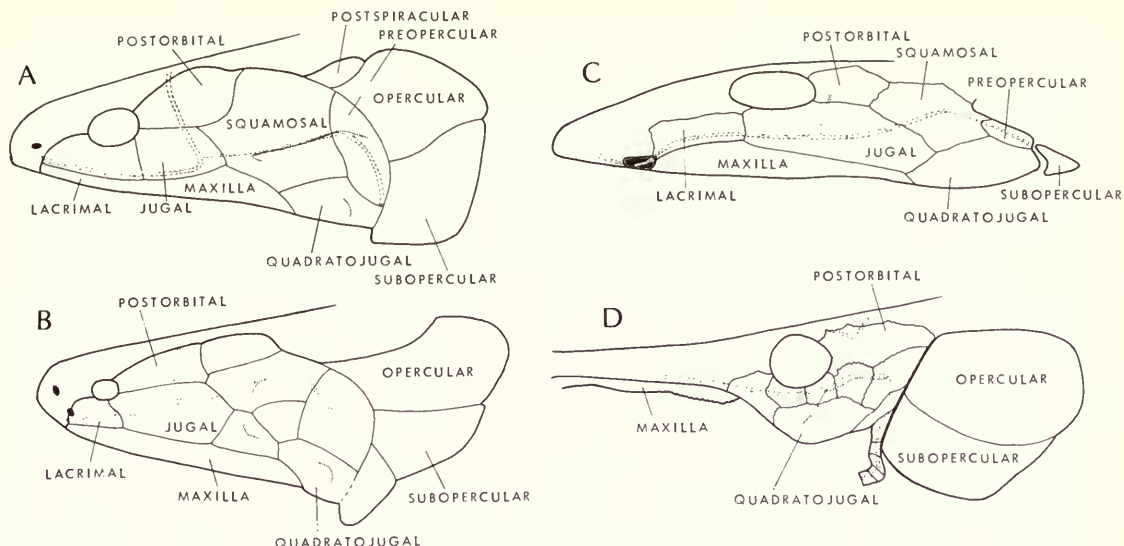


Fig. 78 Cheek bones and operculum. A, *Eusthenopteron foordi* Whiteaves (after Jarvik 1944a); B, *Porolepis brevis* Jarvik (after Jarvik 1972); C, *Ichthyostega* sp. (after Jarvik 1952); D, *Griphognathus whitei* Miles (after Miles 1977). From Rosen *et al.* (1981).

Latimeria; in *Polypterus* and *Acipenser* it lies anterior to the spiracle. It is in contact with the frontals in primitive actinopterygians (*Moithomasia*, *Mimia*, *Cheirolepis*, *Polypterus*) and porolepids (*Holoptychius*, *Porolepis*, *Glyptolepis*, Jarvik 1972: figs 43, 44, 45); with the 'dermosphenotic' /X and intertemporal /Y₁ in osteolepids (*Eusthenopteron*, *Osteolepis*, Jarvik 1972: fig. 61), onychodonts (*Onychodus*) and primitive dipnoans (*Uranolophus*, *Griphognathus*, *Chirodipterus*, Miles 1977: fig. 111); with the parietals in actinistians and with the parietals and supratemporals in *Ichthyostega*. In other primitive tetrapods (loxoematids, temnospondyls) it contacts the postfrontal and supratemporal.

Most workers, however, have failed to recognize that the actinopterygian dermosphenotic is homologous with the tetrapod postorbital, because they have been too concerned in trying to find a one-to-one relationship between the cheek and roofing bones of osteolepids and tetrapods. In primitive actinopterygians (*Cheirolepis*, *Mimia*, *Pteronisculus*; Fig. 88) there are two bones along the otic portion of the temporal sensory canal (supratemporal and intertemporal). There is one in actinistians and porolepids (supratemporal), but in *Powichthys*, *Youngolepis*, osteolepids, onychodonts and dipnoans there are three (supratemporal, intertemporal, and 'dermosphenotic'; Jarvik 1972: fig. 61; Miles 1977: fig. 111, Y₂, Y₁, X). Thus, those authors who have accepted Westoll's (1938) theory that the rhipidistian (osteolepid) frontal is homologous with the tetrapod parietal (see p. 320) consider the osteolepid supratemporal to be homologous with the tetrapod tabular, the intertemporal with the supratemporal, and the 'dermosphenotic' with the tetrapod intertemporal (Panchen 1964: fig. 18; Andrews 1973: fig. 3; Vorobjeva 1977a: fig. 2). They are then able to homologize the osteolepid postorbital with the tetrapod postorbital and so achieve a one-to-one relationship. Säve-Söderbergh (1932: fig. 15), on the other hand, considered that in *Ichthyostega* the dermosphenotic had fused with the postorbital, but that in other amphibians (*Palaeoherpeton*, Säve-Söderbergh 1935: fig. 41; *Aphaneramma*, Säve-Söderbergh 1936: fig. 31A–D) it has fused with the supraorbital. Stensiö (1947: 93; fig. 26) maintained that in the majority of fossil amphibians, including *Palaeoherpeton*, the dermosphenotic had fused with the postorbital and possibly 'one or a couple of adjoining dermopterotic elements too'. Jarvik (1967b: figs 10, 13) supported Säve-Söderbergh as far as *Palaeoherpeton* was concerned, considering the dermosphenotic to have fused with the supraorbital in this form and in 'reptiles', but in temnospondyls he believed it had fused with the intertemporal.

Westoll's (1938) theory concludes that in osteolepids (Fig. 88F) the most anterior element on the main lateral-line (temporal) canal, before the latter turns down onto the cheek (dermosphenotic of Jarvik), is the homologue of the tetrapod intertemporal. Since the intertemporal in tetrapods never has a groove or sulcus for the main lateral-line canal (see for example *Eogyrinus*, Watson 1940: fig. 12), but instead is associated with the supraorbital canal (*Dendroperon*, Steen 1934; *Edops*, Romer & Witter 1942; *Trimerorhachis*, Romer 1947: 247; *Palaeoherpeton*, Panchen 1964: 221; fig. 11), it is difficult to homologize the tetrapod intertemporal with the osteolepid 'dermosphenotic'. Similarly, since the main lateral-line canal always passes through the intertemporal in actinopterygians and osteolepids (*Moythomasia*, Jessen 1968: fig. 1, Dsph; *Eusthenopteron*, *Osteolepis*, Jarvik 1955: fig. 4), where this bone is present, the actinopterygian and osteolepid intertemporal cannot be homologous with the tetrapod intertemporal. This confusion stems from the failure of most authors to recognize that the three bones on the otic portion of the temporal canal of osteolepids are not matched by the three bones in tetrapods. In tetrapods only the supratemporal is associated with the otic portion of the temporal canal. The tetrapod intertemporal, where present, is associated with the supraorbital canal and the tabular with the supratemporal commissure (see below under dermal bones of skull roof, p. 320). In dipnoans there is an additional series of bones between the temporal series and the parietal and median postparietal.

I can now turn to the fusion theory of Säve-Söderbergh (1932: fig. 15; 1935: fig. 41), Stensiö (1947: 93), and Jarvik (1967b: figs 10, 13). As pointed out by Jardine (1970: 345), Nelson (1969a) and Miles (1977: 221), the terms loss and fusion have no clear meaning when applied to phylogeny so that it is not possible to choose objectively between loss and fusion hypotheses. However, there is no need to infer either in this situation because the homologue of the actinopterygian dermosphenotic is clearly recognizable in tetrapods. Many fossil amphibians have been described in which the temporal canal leaves a well-marked lateral groove on the supratemporal before running onto the postorbital, where it then turns down onto the jugal (*Lyrocephalus*, *Metoposaurus*, *Aphaneramma*, Säve-Söderbergh 1937: figs 4A, 12, 31, etc.; *Trimerorhachis*, Case 1935). Thus the tetrapod postorbital is the homologue of the actinopterygian dermosphenotic.

The dermosphenotic/postorbital is loosely attached or hinged to the skull roof in many actinopterygians (*Mimia*, *Stegotrachelus*, *Lepisosteus*, teleosts), *Gyroptychius* (BMNH 50104), osteolepids, actinistians and porolepids, and this is presumed to be the primitive osteichthyan condition.

The 'dermosphenotic' of *Eusthenopteron* (Jarvik 1972: fig. 61) and *Onychodus* is not homologous with the actinopterygian dermosphenotic; instead it is considered topographically homologous with the 'dermosphenotic' (Fig. 89C) or bone X of dipnoans (Miles 1977: fig. 111).

The remaining cheek bones are less contentious. The jugal canal joins the infraorbital canal below the eye on the suborbital portion of the cheek in actinistians, onychodonts, porolepids, osteolepids, dipnoans and tetrapods as it does in some selachians and acanthodians. In actinopterygians the jugal canal is wanting except in *Polyodon* and there is usually a single ossification on the preopercular canal, the preopercular. Exceptions include *Boreosomus*, *Bobasatrania* and *Luganoia* with two ossifications, and *Polyodon* and *Macromesodon* with up to eight tubular bones.

In actinistians, osteolepids and the tetrapods *Ichthyostega* and *Acanthostega* (Säve-Söderbergh 1932: fig. 15; Jarvik 1952: fig. 33a), there are normally two bones on the preopercular-jugal canal, whereas in porolepids (Jarvik 1972: figs 43, 44) there may be three, in dipnoans six (*Neoceratodus*) or seven (*Griphognathus*, Miles 1977: fig. 112), and in tetrapods other than *Ichthyostega* and *Acanthostega* one, the squamosal. By comparing *Ichthyostega* and *Acanthostega* with other osteichthyans, the squamosal is presumed to be homologous in actinistians, tetrapods and osteolepids and the condition in dipnoans, where there are numerous elements, is derived. The actinopterygian condition, with the preopercular extending forwards above the posterior expansion of the maxilla, is likewise derived.

In primitive actinopterygians (*Cheirolepis*, *Mimia*, *Moythomasia*), osteolepids (*Eusthenopteron*, *Osteolepis*, *Eusthenodon*) and some tetrapods (*Ichthyostega*, *Acanthostega*, *Palaeoher-*

peton) the lower margin of the cheek is formed by the quadratojugal and the toothed maxilla. Porolepids and *Polypterus* are similar except that here the preopercular also contributes to the lower margin. In actinistians the quadratojugal is wanting and possibly the maxilla also, and in this latter respect actinistians parallel later dipnoans. Thus a separate quadratojugal (bone 10) is still recognizable in many early dipnoans such as *Dipnorhynchus* (Thomson & Campbell 1971: fig. 7), *Griphognathus* and *Chirodipterus* (Miles 1977: figs 112, 117, bone 10), where it is associated with the cheek pit-line as in actinopterygians, osteolepids, porolepids and some tetrapods (*Palaeoherpeton*, Panchen 1964: fig. 12). Furthermore the bone described as an ectopterygoid in *Griphognathus* by Miles (1977: fig. 57), and which bites outside the lower jaw, is most probably a maxilla (Rosen *et al.* 1981: fig. 7).

The remaining bones of the cheek constitute the infraorbital series which together form the hind and lower borders of the orbit. In primitive actinopterygians (*Mimia*, *Moythomasia*) and in actinistians (*Macropoma*, *Rhabdoderma*, *Latimeria*), osteolepids and porolepids there are only two bones in this series, as in all tetrapods. It seems likely therefore that they are homologous with the jugal and lachrymal. In later actinopterygians the number of bones in the infraorbital series is greatly increased and may be as high as seven in many teleosts (Nelson 1969a: 4). In osteolepids and porolepids the condition is often obscured by ontogenetic fusion of the bones anteriorly. Nevertheless in most described cases at least two bones are recognizable, the jugal and lachrymal of Jarvik (1980). In *Panderichthys* (Vorobjeva 1977b: fig. 2), however, there are as many as four elements. In dipnoans the number of infraorbitals is more variable and in this respect they parallel later actinopterygians. Thus there are four infraorbitals in *Neoceratodus*, five in *Dipnorhynchus*, *Scaumenacia*, *Griphognathus* and *Sagenodus*, and six in *Chirodipterus* and *Dipterus*.

A summary of the dermal bone homologies outlined above is presented in Table 1, p. 323.

Sensory canals of the cheek: summary and discussion

The preopercular canal joins the infraorbital canal behind the orbit and beneath the spiracle in actinistians, porolepids, osteolepids, onychodonts, dipnoans and amphibians. The preopercular canal also joins the infraorbital canal ventral to the spiracle in *Polyodon* but in this instance (as in *Macromesodon*) the cheek plates are reduced and the canal runs in a series of tubular ossicles, a condition which is assumed to be secondary (Stensiö 1947). This connection between the preopercular and infraorbital sensory canals is generally referred to as the jugal line or canal (hyomandibular line; angular-jugal line; supramaxillary line) since in sharks it often differentiates as an independent line (Rudd 1920). In sharks the jugal line is invariably connected to the infraorbital canal from which it may also develop (Holmgren 1940: 85). Usually the jugal canal is not joined posteriorly to the preopercular canal but in some specimens of *Chlamydoselachus* and in *Torpedo* it links the infraorbital and preopercular canals (Holmgren 1942: fig. 19). The jugal canal also grows out from the postorbital portion of the infraorbital canal in *Neoceratodus* (Allis 1934: 369), but in amphibians (Platt 1896, Stone 1922) this connection is achieved by a branch of the preopercular canal growing forwards and downwards across the cheek to meet the infraorbital canal. The preopercular canal is also joined to the infraorbital canal by the jugal canal in many acanthodians and placoderms and this is presumed to be the primitive gnathostome condition.

In actinopterygians, where there is no connection between the two canals, there is a horizontal pit-line in the position of the jugal canal which is similarly innervated by a branch of the mandibular nerve (hyoideo-mandibularis of Pehrson 1947). This pit-line is not found in other groups and it is also missing in *Polyodon*; it is generally considered to be the homologue of the jugal canal of other forms (Stensiö 1947). The horizontal pit-line arises from the upper part of the preopercular canal in *Polypterus* and *Amia* (Allis 1889; Pehrson 1947) and remains intimately connected with it in both embryo and adult. Traces of the anterior limits of the horizontal pit-line are found on the maxilla of *Polypterus* (Jarvik 1947: fig. 1A) and *Moythomasia*.

A further pit-line is present in many osteichthyans, the vertical pit-line (or postmaxillary line, Stensiö 1947). This line is usually in two parts and the dorsal component meets the horizontal

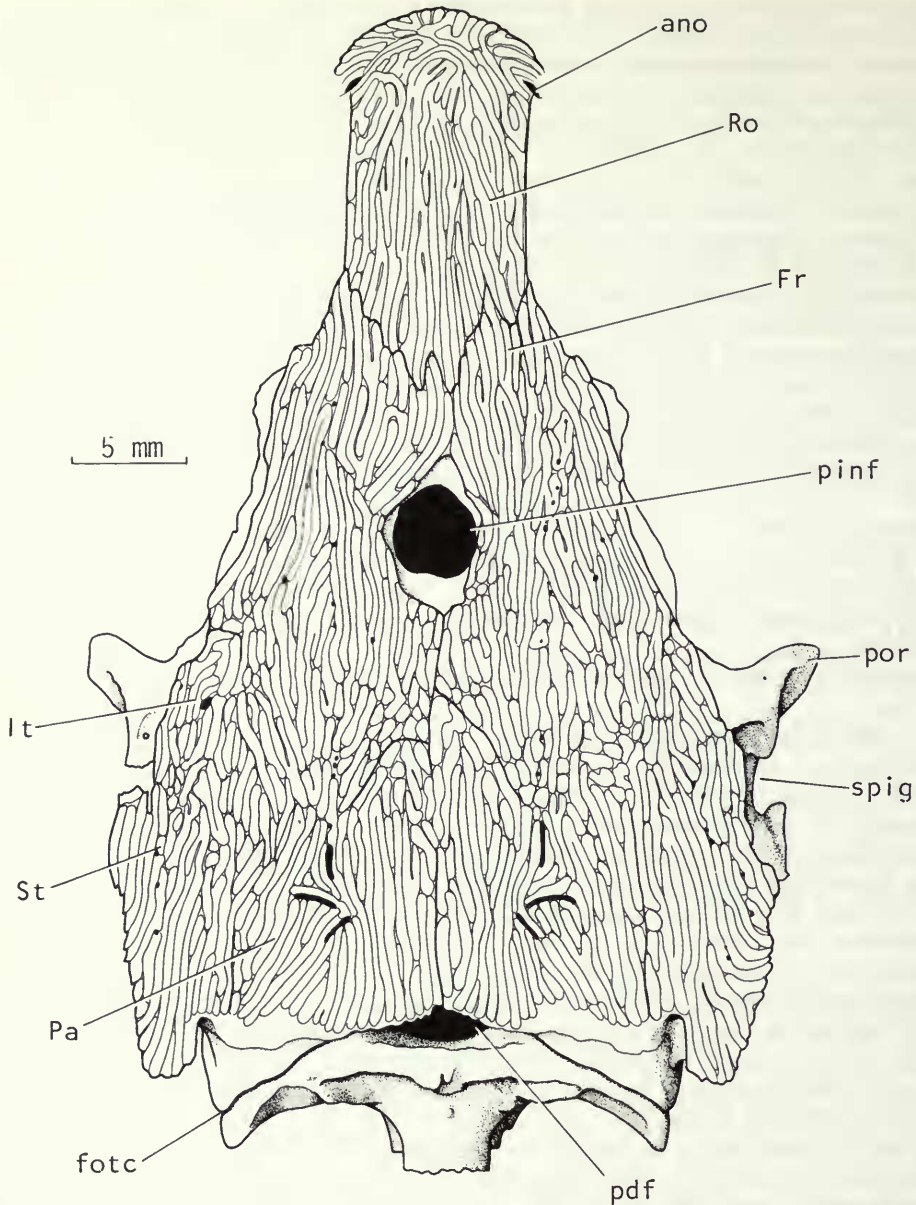


Fig. 79 *Mimia toombsi* Gardiner & Bartram. Neurocranium and attached dermal bones in dorsal view, from BMNH P.53243.

pit-line to give a >-shaped structure in primitive actinopterygians (*Mimia*, *Polypterus*). The ventral part of this line in actinopterygians crosses the quadratojugal when this bone lies near the surface (*Mimia*, *Polypterus*, *Pteronisculus*). In more advanced actinopterygians (*Lepisosteus*, *Amia*) the vertical pit-line is in one piece. The vertical pit-line is also in two parts in some actinistians (*Rhabdoderma*), porolepids (*Holoptychius*), osteolepids (*Eusthenopteron*), some dipnoans (*Dipterus*) and a few primitive amphibians (*Palaeoherpeton*), with the ventral portion crossing the quadratojugal where this bone is present. The line is single in *Griphognathus*, *Neoceratodus* and *Protopterus*. The vertical pit-line meets or crosses the jugal canal in sharks (*Chlamydoselachus*), actinistians (*Nesides*, *Rhabdoderma*), osteolepids (*Eusthenopteron*) and



Plate 1 *Mimia toombsi* Gardiner & Bartram. Braincase in dorsal view, from P.56505, $\times 11\frac{1}{2}$.

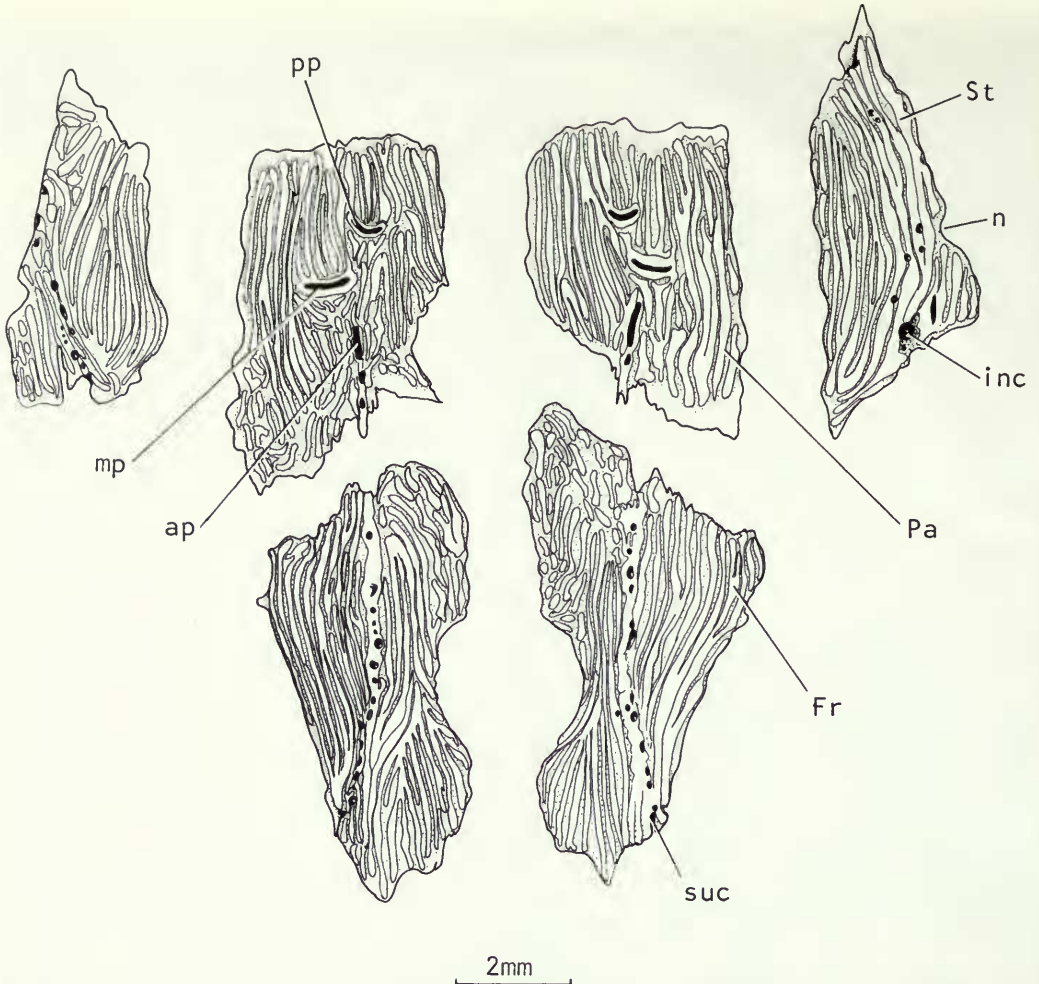


Fig. 80 *Mimia toombsi* Gardiner & Bartram. Dermal bones of the skull roof in dorsal view (intertemporal missing), from BMNH P.56473.

dipnoans (*Griphognathus*, *Protopterus*). The absence of a squamosal bone and a jugal sensory canal are considered autapomorphic for actinopterygians.

Dermal bones of the skull roof

Mimia toombsi

The dermal bones on the dorsal surface of the neurocranium anterior to the occipital fissure are closely applied to the dorsal neurocranial surface. Even the nasals may have a fragile attachment at points where the delicate perichondral nerve canals join the underside of the supraorbital sensory canal (Pl. 1). The only areas where this attachment is less than secure is where the perichondral lining of the neurocranial roof is interrupted posteriorly around the lateral cranial canal and anteriorly in front of the pineal foramen.

The parietal is roughly rectangular in outline, somewhat longer than broad and with its radiation centre beneath the middle pit-line. It has a zigzag suture anteriorly with the frontal. Ventrally two sets of nerve foramina presumably served for branches of the glossopharyngeal nerve (fb.IX, Fig. 81) to the middle pit-line and for branches of the vagus (fb.X, Fig. 81) to the

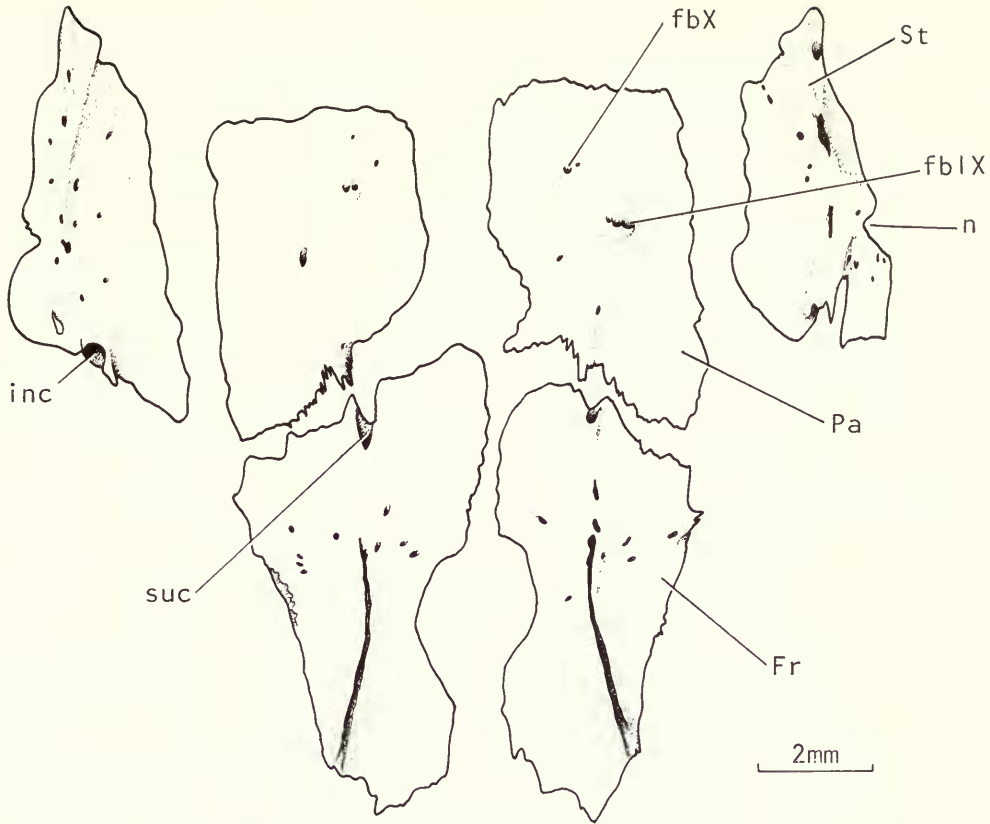


Fig. 81 *Mimia toombsi* Gardiner & Bartram. Dermal bones of the skull roof in ventral view (intertemporal missing), from BMNH P.56473.

posterior pit-line. The anterior pit-line is continuous with the supraorbital canal which leaves the parietal through a tongue-shaped projection of the anterior margin.

The largest element of the dermal roof is the paired frontal which tapers to a point anteriorly. Posteriorly it forms a slight overlap with the parietal. The radiation centre is nearer the posterior than anterior margin, at the level of the rear of the pineal foramen. The supraorbital canal pierces the radiation centre. The anteromedial margin of the frontal has a zigzag suture with the rostral while the anterolateral corner sutures with the nasal. Ventrally the passage of the supraorbital sensory canal is marked by a rounded ridge which may have a slit-like opening anteroventrally (Fig. 81).

The supratemporal is a long, narrow bone which is sutured medially to the parietal and anteriorly to the intertemporal. There is a small notch in its lateral margin (n, Figs 80, 81) dorsal to the head of the hyomandibula. This notch, present in the lateral margin of the intertemporal of many actinopterygians (*Cheirolepis*, *Pteronisculus*, *Elonichthys*, *Moythomasia*), was said by Aldinger (1937: 249) to be related to the underlying fossa bridgei and by Jessen (1968: fig. 1) to be the spiracular opening. But there is no fossa bridgei in *Mimia* or *Moythomasia* and the spiracular opening is between the intertemporal, supratemporal and dermosphenotic. Instead I postulate that this notch allowed the head of the hyomandibula greater flexibility in respiratory movements. The supratemporal is traversed by the otic part of the main lateral-line canal which passes through the radiation centre. This centre lies just behind the notch in the lateral margin. Anterolaterally a flange of the supratemporal forms the posterolateral margin of the spiracular opening (Fig. 82).

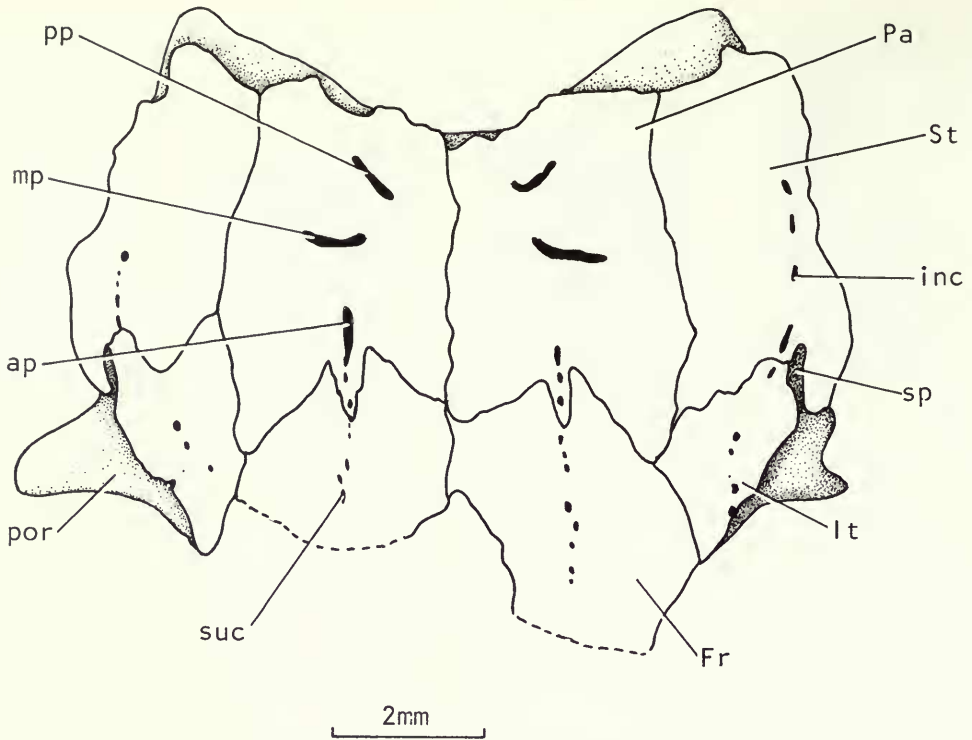


Fig. 82 *Mimia toombsi* Gardiner & Bartram. Otic and orbitotemporal regions of neurocranium and attached roofing bones in dorsal view, from BMNH P.53259.

The intertemporal is a small triangular bone sitting above the postorbital process. It sutures with the parietal and supratemporal posteriorly and with the frontal medially. Its radiation centre is pierced by the main lateral-line canal and lies near the posterior margin. The passage of the sensory canal through both temporal bones is marked ventrally by a rounded ridge.

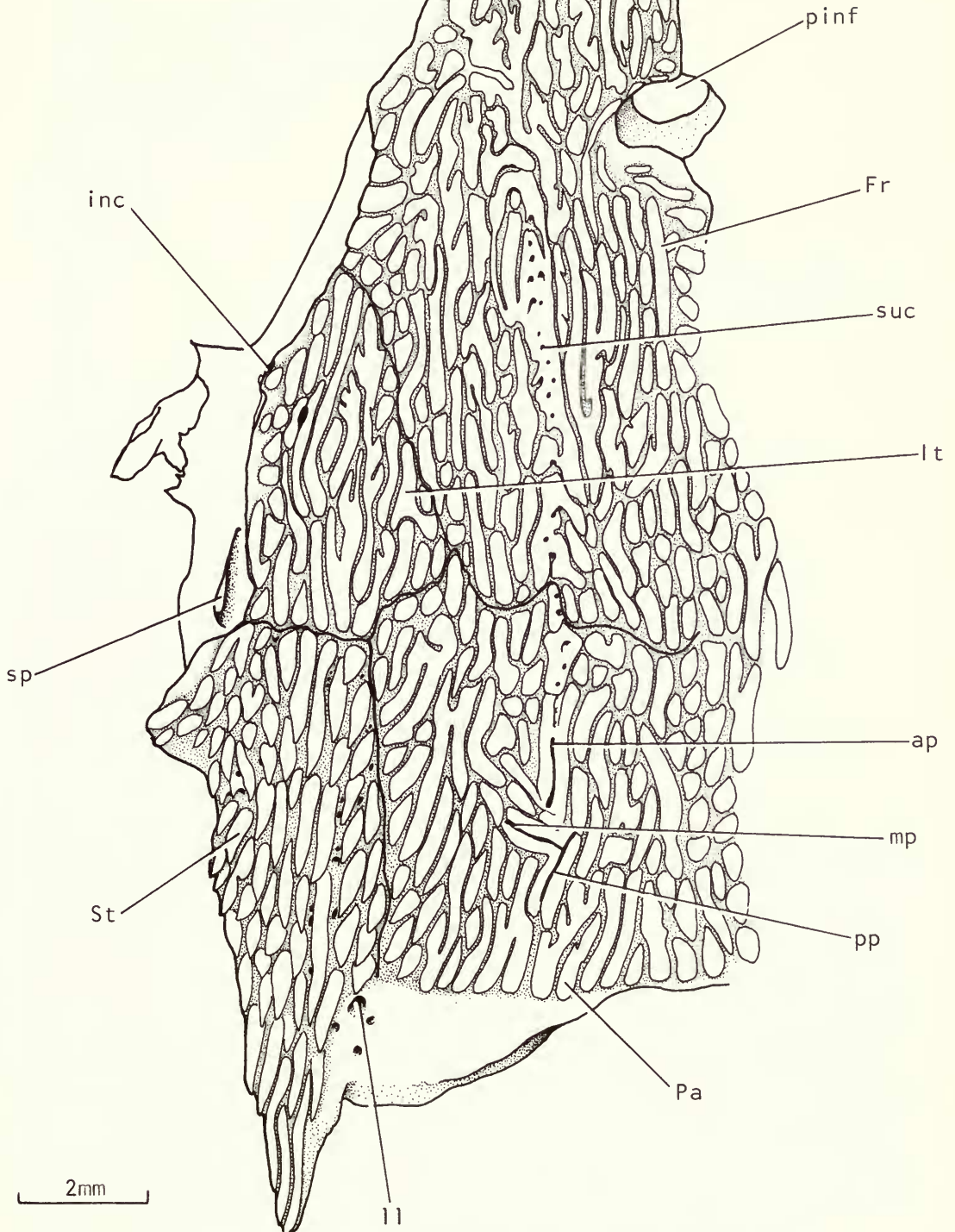
The extrascapular series consist of a single pair of bones which just meet in the midline. Anteriorly the extrascapular sits on the slightly bevelled transverse margin of the parietals. Posteriorly and laterally the extrascapular overlies the occipital region of the neurocranium, covering the posterior dorsal fontanelle and part of the occipital fissure. The supratemporal commissure pierces the bone in a transverse direction and the cephalic division of the main lateral-line runs in a longitudinal direction. The radiation centre is situated at the confluence of these two canals. A posterolateral peg-like projection (Figs 84, 85) of the extrascapular passes under the post-temporal, while its posterior margin rests on an anterior flange of the post-temporal.

Moythomasia durgaringa

The parietals and frontals are very similar to those of *Mimia* (Fig. 83). However, the posteroventral margin of the parietal is more shelf-like than in *Mimia* and more intimately fused with the underlying neurocranium. The posterior corner of the supratemporal is also more markedly pointed. The extrascapular series consists of two pairs of bones, a smaller medial pair and a much larger lateral pair (Fig. 87).

The lateral extrascapular contacts the parietal anteriorly, but laterally sits on an inwardly-directed flange of the supratemporal. The medial extrascapular comprises two components: an anterior plate of bone and a posterior tubular portion for the supratemporal commissure.

Fig. 83 *Moythomasia durgaringa* Gardiner & Bartram. Left otic and orbitotemporal regions of neurocranium and attached roofing bones in dorsal view, from BMNH P.53221.



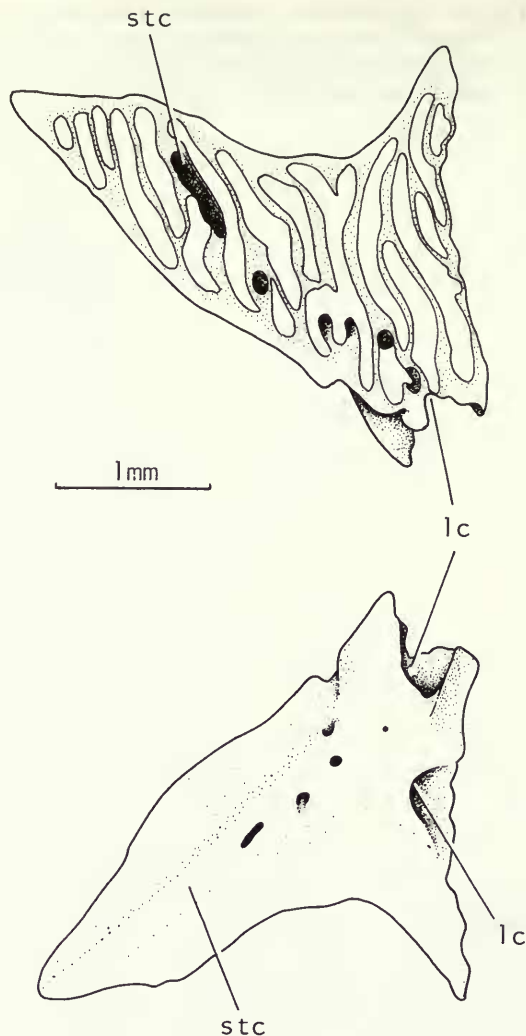


Fig. 84 *Mimia toombsi* Gardiner & Bartram.
Right extrascapular in dorsal (above) and
ventral views, from BMNH P.54498.

Dermal bones of skull roof: summary and discussion

1. Homologies of dermal bones of skull roof

The osteichthyan dermal roofing bones form two distinct patterns (Rosen *et al.* 1981). The more primitive is believed to be that found in actinopterygians, osteolepiforms, porolepiforms and actinistians, in which the paired frontals and parietals form the major constituents of the skull roof and the parietals reach the posterior limits of the otic region of the underlying neurocranium. The pineal foramen is invariably situated between the frontals. The alternative, derived pattern is seen in dipnoans and tetrapods (Fig. 89), where there is a cluster of at least two pairs of bones behind the parietals and the pineal foramen lies either between the parietals or just anterior to them (*Dipnorhynchus*, later tetrapods).

The two pairs of bones covering the dorsal side of the otic region in actinopterygians, osteolepiforms, porolepiforms and actinistians were originally called frontals and parietals because they appeared to be homologous with those bones in mammals. The cluster of six bones behind the parietals in primitive tetrapods were called postparietals, tabulars and supratemporals. Lying behind these skull roofing bones and therefore not attached to the under-

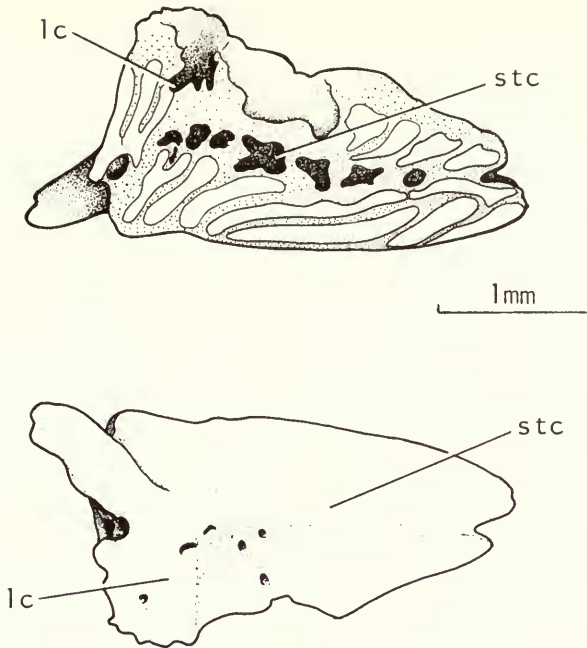


Fig. 85 *Mimia toombsi* Gardiner & Bartram. Left extrascapular in dorsal (above) and ventral views, from BMNH P.56497.

lying neurocranium is a series of scale bones or extrascapulars (Jollie 1981). This series is missing in tetrapods.

In the search for tetrapod origins it was necessary to reconcile these two distinct dermal roofing bone patterns, because osteolepiforms were thought to include the tetrapod ancestor. Thus Säve-Söderbergh (1932) proposed that the ancestral dermal roof of crossopterygians and tetrapods must have contained two pairs of frontals and parietals and that the tetrapod parietal and postparietal should be regarded as fronto-parietal and parieto-extrascapular respectively. The assumption that the extrascapular series of scale bones could in some way become intimately associated with the otic region of the neurocranium had already been proposed by Watson & Day (1916) when they homologized the crossopterygian medial extrascapular with the tetrapod postparietal and the lateral extrascapular with the tabular. This theory, subsequently modified by Säve-Söderburgh (1935, 1936) and championed by Jarvik (1967b: 205), demands that a transverse series of scale bones moved forward onto the neurocranium. As Rosen *et al.* (1981: 222) have pointed out, the dermal roofing bones in osteichthyans (and placoderms – see Jarvik 1967b: fig. 3) are frequently attached to the underlying neurocranium by descending laminae of membrane bone. Where laminae are missing the dermal bones may be equally tightly attached to the underlying perichondral bone as in *Mimia*, *Moythomasia* and *Eusthenopteron* (Jarvik 1975: fig. 13). It therefore appears unlikely that these dermal roofing bones would have been able to move forward on the otic region to make room for the extrascapular series. Moreover, in many dipnoans the cluster of five roofing bones (behind the parietals) is followed by a series of extrascapular scale bones which lie loosely behind them (Miles 1977: figs 111, 116, 118), free of the underlying otic region of the neurocranium.

An alternative theory to that of Watson & Day (1916) was Westoll's (1936, 1938) proposition that the crossopterygian frontal was homologous with the tetrapod parietal. Westoll's theory demands the reverse of Watson & Day's: that is, it assumes that there was a backward movement of the parietals, again without regard to the underlying neurocranium. To accept Westoll's theory is to deny the presence of frontals in all bony fishes with the exception of the osteolepids, *Elpistostege* and *Panderichthys* and certain dipnoans (*Dipterus*, *Uronemus*,

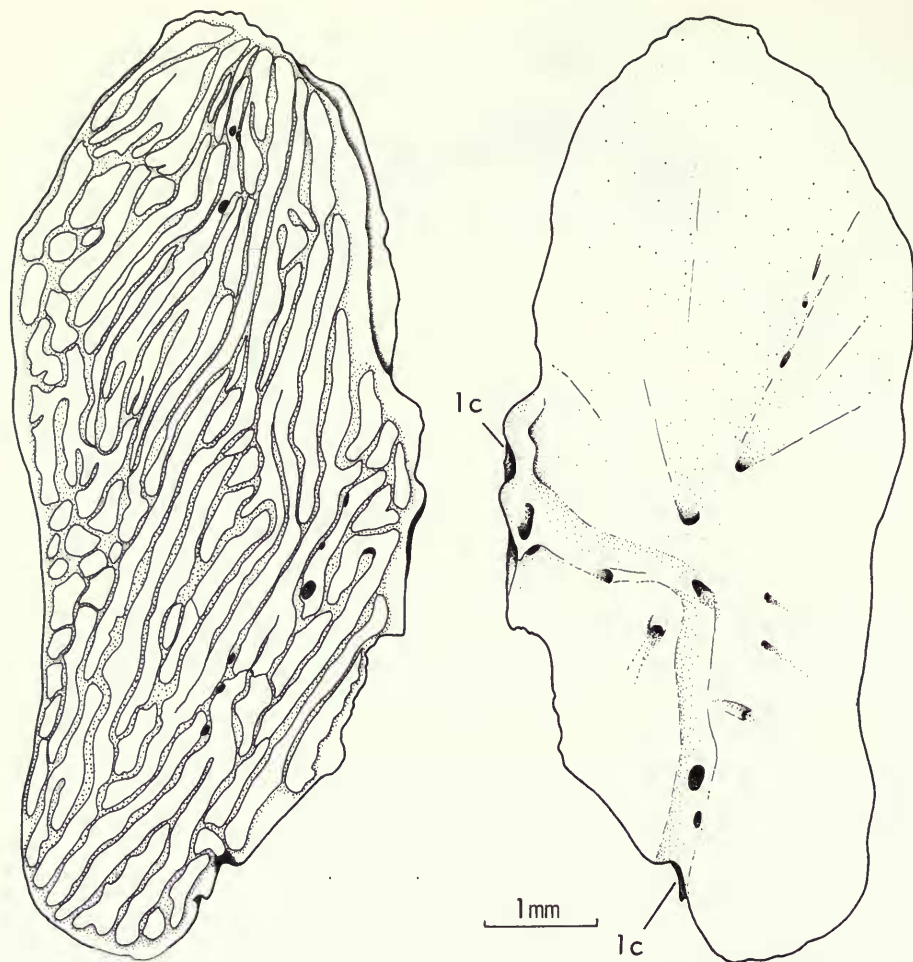


Fig. 86 *Mimia toombsi* Gardiner & Bartram. Right post-temporal in dorsal (left) and ventral views, from BMNH P.56498.

Rhinodipterus, *Scaumenacia*, *Ctenodus*). I have suggested (Gardiner 1980) that an extra pair of bones in *Panderichthys* be called postparietals, but they are associated with transverse pit-lines (Vorobjeva 1977b: fig. 2B) and are better homologized with the parietals of *Eusthenopteron*.

The temporal bones (intertemporal, supratemporal /Y₁Y₂) have already been discussed (see p. 311), but it is worth noting that in later actinopterygians (e.g. many palaeoniscids, *Lepisosteus*, *Amia*, teleosts) the two temporal bones are replaced by a single dermopterotic. A single bone similarly occupies this position in *Ichthyostega*, most temnospondyls, and primitive amniotes where it is called the supratemporal. Two temporal bones occur in some loxommatids, a few temnospondyls, anthracosaurs and *Seymouria*.

From the evidence given above it seems that the tetrapod supra- and intertemporal are not homologous with similarly-named bones in other osteichthyans. If this conjecture is correct, then those bones associated with the otic portion of the infraorbital sensory canal in primitive osteichthyans are absent in tetrapods. Support for this suggestion is afforded by living amphibians where the otic part of the infraorbital line is reduced to a single organ (Platt 1896; Stone 1922) and by primitive fossil amphibians where the infraorbital line ends blindly in the postorbital (*Ichthyostega*, *Loxomma*, *Crassigyrinus*, etc.).

Table 1 The positional homologies of dermal skull and cheek bones in Osteichthyans.

Primitive Actinopterygians (<i>Mimia</i> , <i>Moythomasia</i>)	<i>Eusthenopteron</i>	Porolepiformes	Actinistians	Dipnoans	<i>Ichthyostega</i>	Primitive Tetrapods
Frontal	Frontal	Frontal	Frontal	Frontal/E Parietal/C	Frontal Parietal	Frontal Parietal
Parietal	Parietal	Parietal	Parietal	Median postparietal/B	Median postparietal	Postparietal
Dermosphenotic	Postorbital	Postorbital	Postorbital	Postorbital/4	Postorbital	Postorbital
Intertemporal	Dermosphenotic Intertemporal			Dermosphenotic		
				Intertemporal/Y1,X		
Supratemporal	Supratemporal	Supratemporal	Supratemporal	Supratemporal/Y2		Intertemporal
				K		Supratemporal
				Anterior lateral parietal/J	Supratemporal	
				Posterior lateral parietal/I	Tabular	Tabular
Jugal Lachrymal	Jugal Lachrymal	Jugal Lachrymal	Jugal Lachrymal	Infraorbitals/5,6,7,1	Jugal Lachrymal	Jugal Lachrymal
Preopercular	Squamosal Preopercular	Squamosal Preopercular Preoperculo-submandibular	Squamosal Preopercular	8+9a-f	Squamosal Preopercular	Squamosal
Quadratojugal	Quadratojugal	Quadratojugal		10	Quadratojugal	Quadratojugal
Maxilla	Maxilla	Maxilla		Maxilla	Maxilla	Maxilla
Premaxilla	Premaxilla	Premaxilla fused into snout	Premaxilla	Premaxilla fused into snout	Premaxilla	Premaxilla
Nasal	3 Nasals	4-5 Nasals	3 Nasals	4-10 Nasals	Nasal	Nasal
2-4 Extrascapulars	3 Extrascapulars	3 Extrascapulars	3-7 Extrascapulars	3 Extrascapulars		

Behind the parietals and postparietal of actinopterygians, actinistians, rhipidistians and dipnoans lie the transverse series of extrascapular bones. In actinopterygians this series frequently consists of a single pair of bones (e.g. *Cheirolepis*, *Mimia*, *Amia*, *Elops*). In other actinopterygians it comprises two pairs of bones (*Polypterus*, *Moythomasia*, *Lepisosteus*), but in *Acipenser* it is made up of a lateral pair with a much larger median element. A pattern similar to that of *Acipenser* is found in most osteolepids, porolepids, onychodonts and primitive actinistians (*Diplocercides*, *Rhabdoderma*). In later actinistians the number of lateral extrascapulars increases; thus in *Diplurus* there are three lateral pairs and in *Latimeria* there are four pairs as well as the median element. The condition in dipnoans is less clear, although there appears to be a median element and at least one pair of lateral bones in primitive forms (*Grithognathus*, *Chirodipterus*, *Dipterus*, *Scaumenacia*, Jarvik 1968; Miles 1977). An additional pair of scale bones which are not canal-bearing occurs in *Grithognathus* and *Chirodipterus*, whereas in *Dipnorhynchus* there are three pairs of canal-bearing lateral bones and a median element (Thomson & Campbell 1971). Outside the osteichthyans a single pair of scale-like extrascapulars (or postnuchals) has been recorded in a few advanced placoderms such as the coccosteids *Millerosteus* and *Dicksonosteus*, and a median extrascapular is said to be present in the actinolepid *Sigaspis* (Goujet 1973). In the coccosteids the extrascapulars are traversed by the supratemporal commissure. Although the placoderms show a third pattern of dermal roofing bones, little of this pattern matches either of those seen in osteichthyans. However, the presence of large dermal roofing bones with descending laminae and contained tubular sensory canals in at least the presumed primitive placoderms (Miles & Young 1977) is considered synapomorphous for a group including placoderms and osteichthyans.

2. Sensory canals of skull roof

The supraorbital canal joins the infraorbital canal above the eye in most living actinopterygians (*Polypterus*, *Acipenser*, *Polyodon*, *Amia*, *Lepisosteus*, many teleosts). Nevertheless the two canals arise separately and in *Amia* the supraorbital canal anastomoses with the infraorbital by the penultimate primary pore and then continues back onto the parietal (Allis 1889). The two canals remain separate in many primitive actinopterygians such as *Cheirolepis*, *Mimia*, *Moythomasia* and *Elonichthys*, as well as in more advanced forms like caturids, pachycormids and *Leptolepis*.

The canals join behind the eye in actinistians (e.g. *Nesides*, *Rhabdoderma*, *Whiteia*, *Diplurus*, *Latimeria*) and in all described osteolepiforms (e.g. *Eusthenopteron*, *Osteolepis*), porolepiforms (e.g. *Holoptychius*, *Glyptolepis*, *Porolepis*) and *Powichthys*. In dipnoans the canals are separate in *Uranolophus* and *Dipnorhynchus*, but join behind the eye in almost all other forms (*Grithognathus*, *Chirodipterus*, *Dipterus*, *Fleurantia*, *Neoceratodus*, *Protopterus*). Again in many fossil tetrapods (*Trematosaurus*, *Lyrocephalus*, *Batrachosuchus*) the canals remain separate, but in others like *Trimerorhachis*, *Metoposaurus* and in living genera such as *Pelobates* they join behind the orbit. In most selachians (e.g. *Chlamydoselachus*, *Mustelus*, *Torpedo*) and holocephalans (e.g. *Callorhynchus*, *Chimaera*), although the two canals invariably develop independently (Rudd 1920, Holmgren 1940), they join behind the eye in the adult (Garman 1888). In *Laemargus* (*Somniosus*), however, Garman (1888) concluded that the two canals remained separate, but Ewart (1895) showed that the infraorbital and supraorbital canals open to the exterior by a common pore. They agreed that the remaining lines terminated independently on the top of the head in *Laemargus*. In placoderms the infra- and supraorbital canals or lines remain separate in such diverse forms as *Lunaspis*, *Holopetalichthys*, *Romundina*, *Arctolepis* and *Leiosteus*, whereas they may join in a somewhat unusual fashion in *Coccosteus* and *Ctenurella* (Miles & Young 1977). The pattern of the pit-lines on the head of arthrodires and phyllolepid, where three sets of lines converge (supraorbitals, infraorbitals/central canal, posterior pit-lines) is very similar to that in the selachian *Laemargus*. This similarity may be regarded either as a synapomorphy of placoderms and *Laemargus* or as the retention of the primitive gnathostome condition. The presence of three pairs of converging pit-lines on the parietals of actinopterygians (and their innervation, Allis 1922, Pehrson 1947) and on the posterior parietals of many fossil dipnoans (*Grithognathus*, *Chirodipterus*, Miles

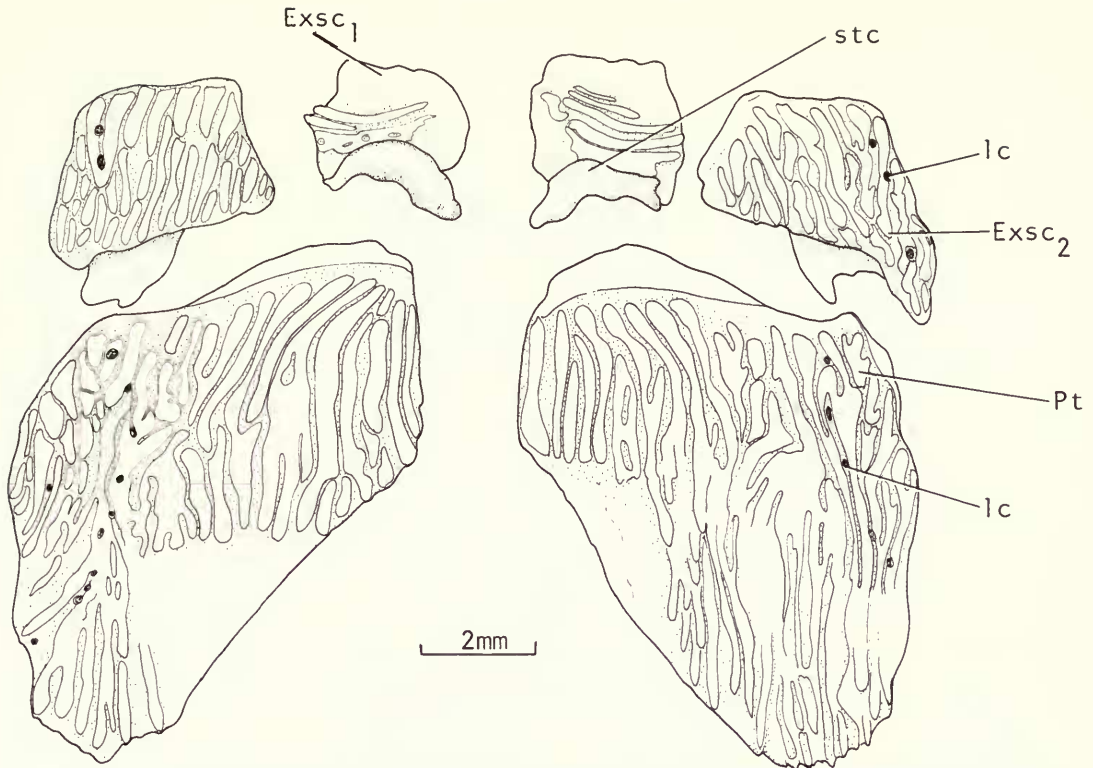


Fig. 87 *Moythomasia durgaringa* Gardiner & Bartram. Extrascapulars and post-temporals in dorsal view, from BMNH P.53221.

1977: figs 113, 116; *Rhinodipterus*, *Scaumenacia*) convinces me that the latter view is the more likely.

In acanthodians the infra- and supraorbital canals always remain separate (e.g. *Euthacanthus*, *Ischnacanthus*, *Diplacanthus*, *Homalacanthus*, *Acanthodes*, Watson 1937), and in *Diplacanthus* the infraorbital canal is continued up on the top of the head as the central sensory line. In this respect *Diplacanthus* resembles placoderms and *Laemargus* and this must be the primitive condition. Thus we may conclude that primitively in gnathostomes the infraorbital and supraorbital canals were separate.

Lower jaw

Mimia toombsi

The Meckelian cartilage is ossified throughout its length in presumed older individuals. In less well ossified specimens there are two perichondral ossifications, one anteriorly and one posteriorly. In others the perichondral covering is complete apart from the glenoid fossa and there are endochondral cores anteriorly and posteriorly. These ossifications are the mentomeckelian and articular bones. Separate mentomeckelian and articular bones are only distinguishable in a few specimens (cf. BMNH P.56473) and even so the mentomeckelian usually has the two anterior coronoids closely applied to its medial surface.

Where ossification is complete all the exposed surfaces of the Meckelian bone are perichondrally ossified except in the glenoid fossa. The bulk of the articular region is formed of dense endochondral bone. Posterodorsally the glenoid fossa is represented by two distinct depressions which match the double condyle of the quadrate. Posteriorly and ventrally the

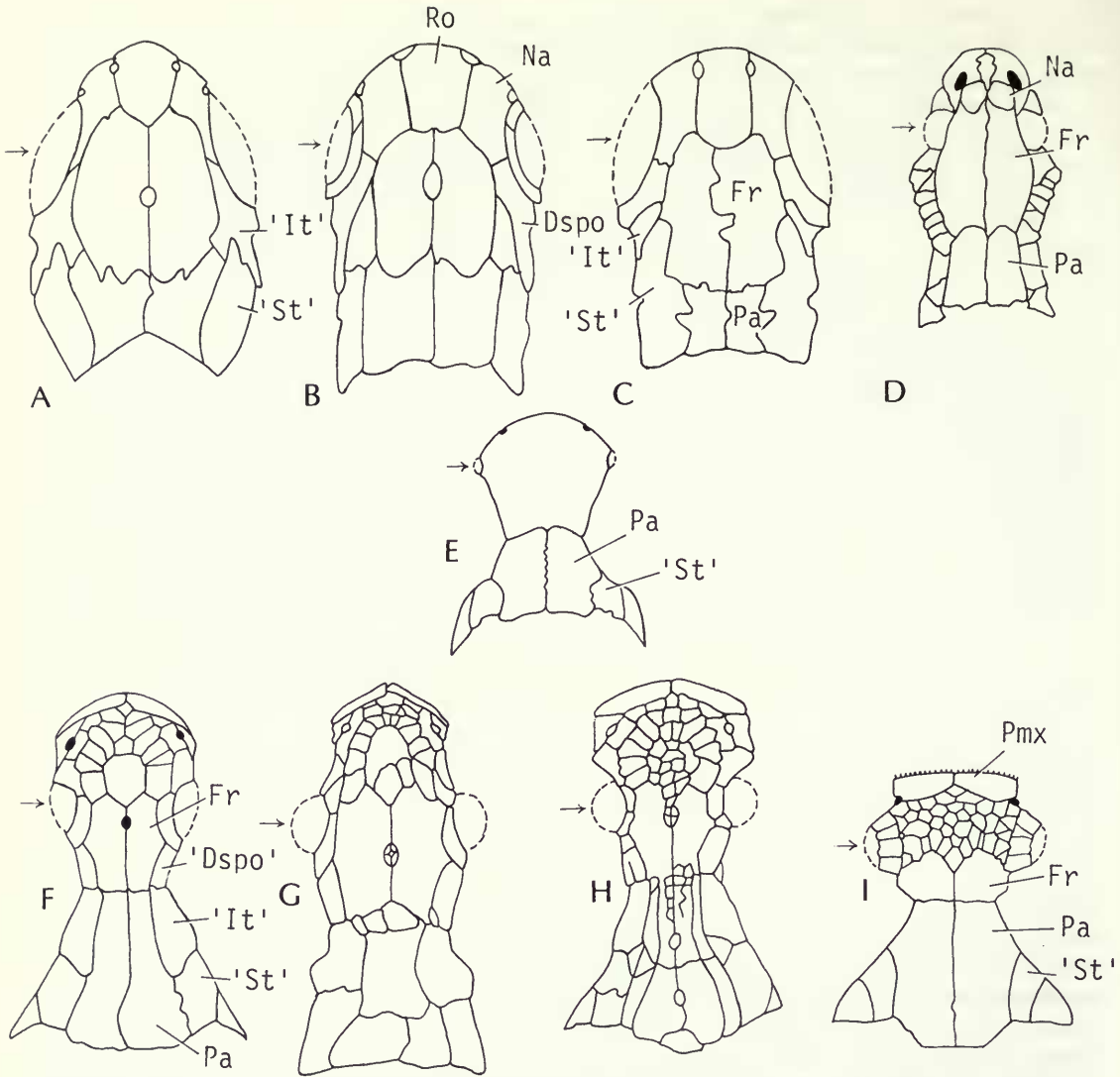


Fig. 88 Skull roofs. A, *Kentuckia deani* (Eastman) (from Rayner 1951); B, *Moythomasia nitida* Gross (from Moy-Thomas & Miles 1971); C, *Pteronisculus magnus* (Nielsen) (from Nielsen 1942); D, *Polypterus* sp. (from Schmalhausen 1968); E, *Porolepis brevis* Jarvik (from Jarvik 1972); F, *Eusthenopteron foordi* Whiteaves (from Jarvik 1967b); G, *Eusthenopteron*, composite, showing variations in bone patterns (from Jarvik 1967b); H, composite showing maximum number of separate bones observed in *Osteolepis*, *Thursius*, and *Gyroptychius* (from Jarvik 1948); I, *Holoptychius* sp. (from Jarvik 1972). Scale bones at back of braincase omitted. From Rosen *et al.* (1981).

articular is free of any dermal bone investment, as is the greater part of the ventromedial face of the Meckelian bone.

There is a distinct groove (gmand.ext.VII, Fig. 91) behind the lateral corner of the glenoid fossa. The groove continues anteriorly on the medial surface of the dentary. Several foramina on the dentary open into this groove, and presumably served for the innervation of that section of the mandibular sensory canal. An identical groove has been recorded in *Pteronisculus* (Nielsen 1942: figs 38, 40, sm). By comparison with *Polypterus* (Allis 1922) the groove is presumed to

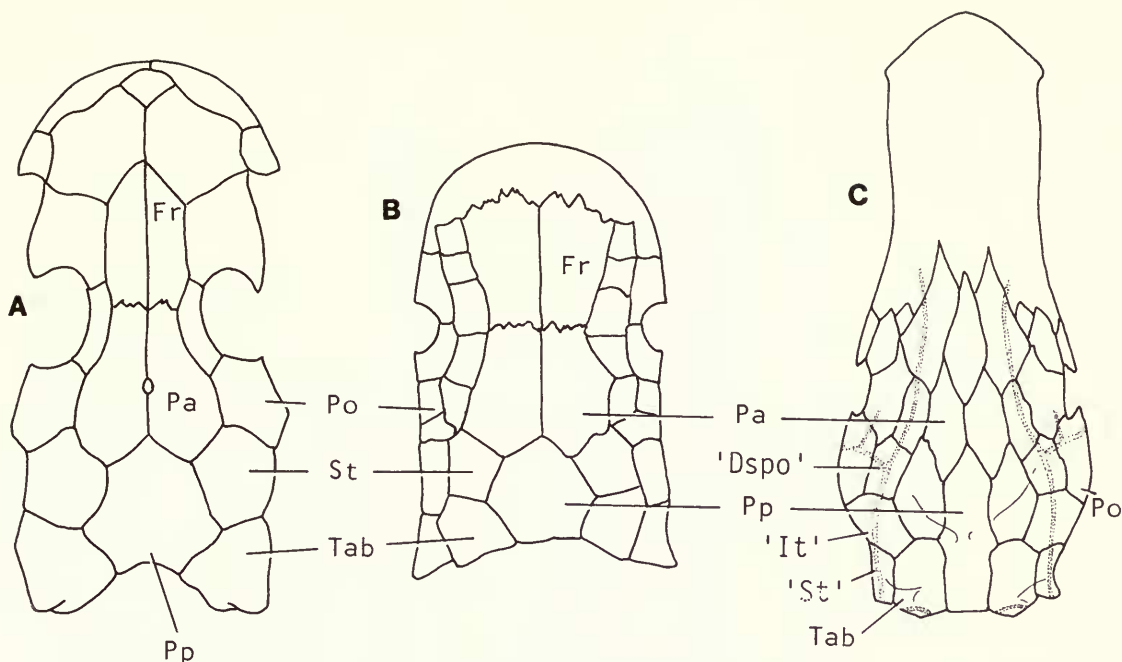


Fig. 89 Skull roofs. A, *Ichthyostega* sp. (from Romer 1966); B, *Scaumenacia* sp.; C, *Griphognathus whitei* Miles (from Miles 1977).

have carried the external mandibular branch of the facial nerve. Three or four large foramina (fmand.V, Fig. 91) in the ventral margin of the Meckelian bone, anterior to the junction of the angular and dentary, presumably served for the passage of branches of the trigeminal nerve from the adductor fossa into this groove, as in *Polypterus*.

On the medial face of the Meckelian bone and a little way in front of the top of the previously mentioned groove is a distinct foramen (fmand.int.VII, Fig. 91). This foramen leads into a canal which passes anterodorsally between the prearticular and the perichondral covering of the Meckelian bone and then between the posterior coronoid and the perichondral covering of the Meckelian bone. The canal finally opens into the groove between the coronoids and the dentigerous edge of the dentary, as in *Polypterus*. The canal therefore must have transmitted the internal mandibular branch of the facial nerve. A similar canal has been described in *Pteronisculus*, *Birgeria* (Nielsen 1942, 1949) and other palaeoniscids (Poplin 1974: fig. 40).

Anteriorly the Meckelian bone is densely ossified in the region of the mentomeckelian ossification. The mentomeckelian bone extends back beneath the coronoids where it merges indistinguishably with the anterior end of the articular. Beneath the coronoids the mentomeckelian bone is ridged in an anteroposterior direction. This ridging is presumed to represent the area of origin of the geniohyoideus muscle, this being precisely its area of origin in *Polypterus* (Allis 1922: 255). The same ridges may also be for the intermandibular muscles. In the same region of *Pteronisculus* (Nielsen 1942: 165) there is a series of shallow depressions.

The external surface of the mandible is composed of two dermal bones, the dentary and the angular. Together they form the outer boundary of the adductor fossa. The angular forms the hind margin of the mandible and is roughly triangular in outline. The mandibular canal pierces it from end to end, passing through the radiation centre which is marked by a slot-like pit-line. In its posterior margin the angular has a small depression (pch1, Fig. 90). This is presumed to have been the origin of the ceratohyal ligament, as in *Polypterus* (Allis 1922: 246). A similar ligament in *Lepisosteus* (Wiley 1976) has its origin on the retroarticular. Anterodorsally the angular is joined to the dentary by an interdigitating suture. The angular and dentary in this region are

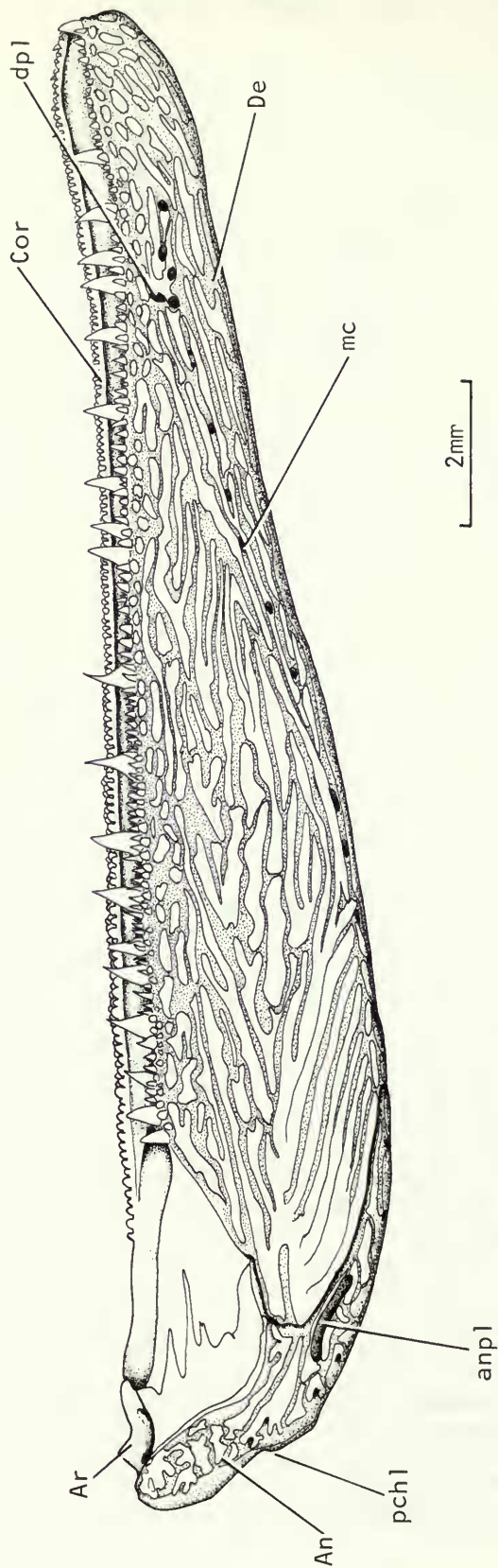


Fig. 90 *Mimia toombsi* Gardiner & Bartram. Right lower jaw in lateral view, from BMNH P.56498.

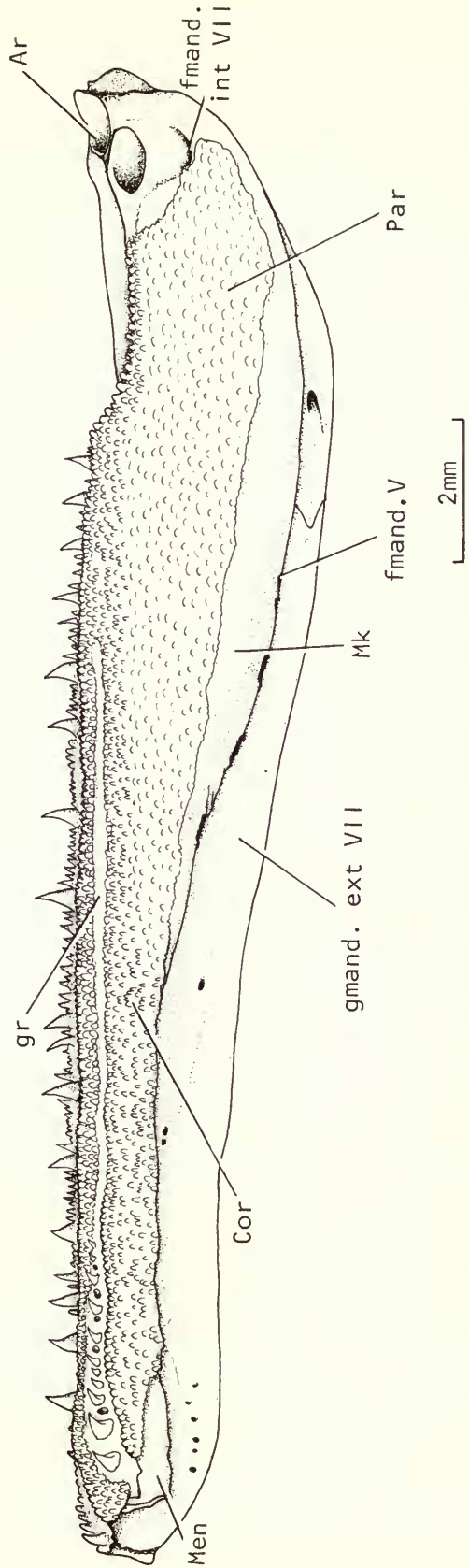


Fig. 91 *Mimia toombsi* Gardiner & Bartram. Right lower jaw in medial view, from BMNH P.56498.

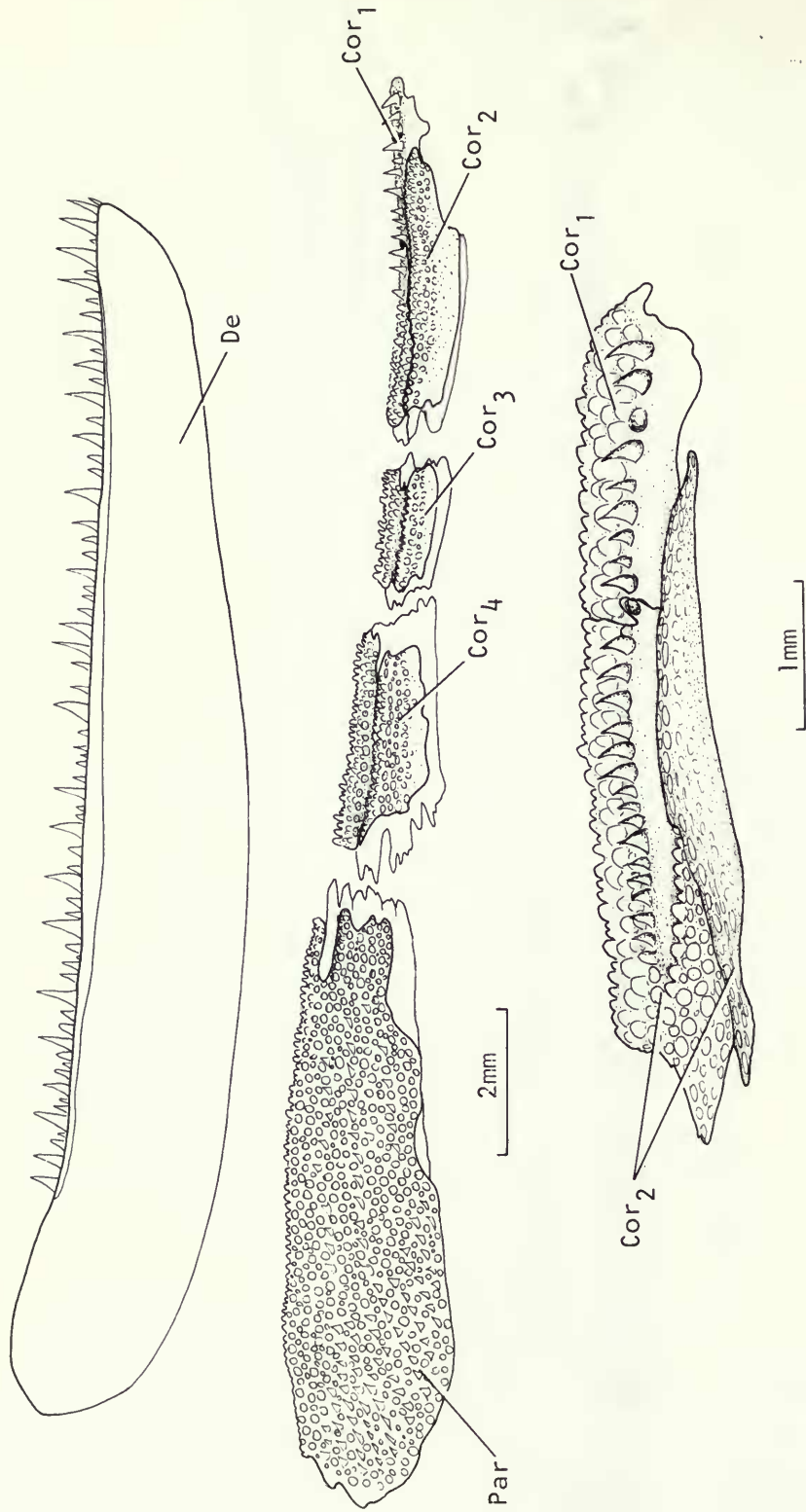


Fig. 92 *Mimia toombsi* Gardiner & Bartram. (A), left dentary, and associated tooth plates of an incompletely ossified individual, in medial view; (B), anterior coronoids more highly magnified; all from BMNH P.56473.

devoid of ornamentation and the triangular area of smooth bone represents exactly that part of the mandible permanently overlapped by the maxilla. The radiation centre of the angular lies near the posterodorsal corner.

The dentary is very long and its anterior end curves medially. It bears on its dorsal edge a row of sharp, stout teeth, and outside this row there are numerous smaller teeth. The larger teeth possess an apical cap of acrodin (Pl. 4, c). The dentary overlaps the angular posteroventrally and is traversed for almost its full length by the mandibular sensory canal. The canal enters the dentary at its most ventral point of contact with the angular and from there the canal rises at a low angle up through the dentary, changing direction somewhat anteriorly. Where the canal changes direction there is a group of five pores and this represents the radiation centre. Two of these pores form a pit-line and in other specimens a distinct anterodorsal slot is developed in this region. A dentary pit-line has only been recorded elsewhere in *Polypterus* (Jarvik 1947: fig. 1A). An oral sensory canal is found in the surangular of dipnoans.

By far the largest dermal bone on the medial side of the mandible is the prearticular, which covers the dorsal and much of the medial face of the Meckelian bone in the region of the adductor fossa. Posteriorly this bone ends on the lateral face of the Meckelian bone just behind the glenoid fossa. It extends anteriorly for half the total jaw length, much as in *Pteronisculus*. The prearticular is gently rounded dorsoventrally, with its dorsal surface forming a horizontal lamina in front of the adductor fossa. This lamina contacts the horizontal lamina of the dentary laterally, while anteriorly it bears a groove which is continuous with that on the coronoids (gr, Fig. 91). The groove is a mirror image of a similar groove on the dermopalatines. The whole of the outer surface of the prearticular is covered by a shagreen of small rounded teeth similar to those on the palate. The radiation centre lies dorsally, immediately anterior to the adductor fossa. Anteriorly the prearticular is joined to the fourth coronoid by a deeply interlocking zigzag suture. Similar sutures are present between successive coronoids. The coronoid series consists of four bones of which the posterior is the largest. The third and fourth coronoids are of the same general shape with a gently rounded medial lamina and a grooved, stouter horizontal lamina. Their radiation centres lie in the middle of the bones in the anteroposterior groove. They are covered with a similar shagreen of rounded teeth as is found on the prearticular. The two anterior coronoids are invariably closely applied to the underlying mentomeckelian bone and the first coronoid does not possess a medial lamina. Instead the tuberculated lamina of the second coronoid (Fig. 92) is produced anteriorly and overlies the posteromedial surface of the first coronoid. A similarly-situated bone in the anterior part of the mandible of *Pteronisculus* (Nielsen 1942: figs 38, 39, 40, Mmd), said by Nielsen to contain both an endochondral and a dermal component, may be reinterpreted as the medial lamina of a coronoid fused to the underlying mentomeckelian, as in *Mimia*.

The two anterior coronoids have, in addition to their small teeth, a row of larger, acutely pointed teeth along the outside of the aforementioned groove.

Moythomasia durgaringa

The mandible of *Moythomasia* is similar to that of *Mimia* but differs in the presence of a supra-angular.

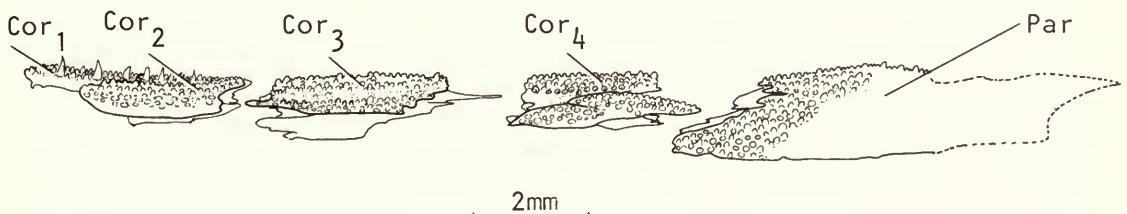


Fig. 93 *Mimia toombsi* Gardiner & Bartram. Dermal tooth plates of the right lower jaw of an incompletely ossified individual in medial view, from BMNH P.56473.

The prearticular consists of two ossifications: there is a separate, much smaller, posterior ossification overlying the entrance to the canal for the internal mandibular branch of the facial nerve. The prearticular teeth are confined to the posterior and dorsal margins of the first prearticular and the medial laminae of the coronoids are mostly toothless. The supra-angular is a stout ossification which forms the lateral border of the adductor fossa. It overlaps the dentary and prearticular anteriorly and the angular ventrally. Posterodorsally it is attached to the articular. All four coronoids bear a row of much larger, acutely pointed teeth. These are continuous with a few similar teeth on the anterior portion of the first prearticular.

Lower jaw: discussion

1. Meckelian ossifications

In presumed juveniles of *Mimia* and *Moythomasia* a thin perichondral sheath is present round the anterior and posterior ends of Meckel's cartilage, much as in *Acanthodes* (Miles 1973a, Jarvik 1977). Later an endochondral core forms in the articular posteriorly and in the mentomeckelian bone anteriorly. Eventually these two ossifications meet and the whole cartilage is endochondrally and perichondrally ossified. It is then usually referred to as the Meckelian bone. A fully-developed Meckelian bone is characteristic of most adult palaeoniscids, including *Mimia*, *Moythomasia*, *Pteronisculus* and *Boreosomus*, of *Australosomus*, of osteolepids such as *Eusthenopteron* and *Panderichthys*, porolepids such as *Glyptolepis*, and primitive dipnoans (*Griffithichthys*, *Chirodipterus*, *Holodipterus*, *Melanognathus*, *Dipterus*). Two discrete ossifications separated by cartilage are characteristic of *Polypterus*, parasemionotids, *Pholidophorus germanicus*, fossil actinistians such as *Rhabdoderma*, *Diplocercides*, *Coelacanthus* and *Coccoderma*, and tetrapods such as *Ichthyophis*, *Cryptobranchus* and *Lacerta*. But in *Lepisosteus*, most teleosts and *Latimeria* the posterior end of Meckel's cartilage possesses two ossifications, the articular proper and the retroarticular, whereas in *Amia* there are three (two articulars and a retroarticular). There are also two posterior ossifications (in tandem) in several fossil actinistians (*Macropoma*, *Laugia*, *Whiteia*), but in larger specimens of *Whiteia* and in *Rhabdoderma* there is only a single ossification (P. L. Forey, personal communication). Nelson (1973) concluded that the presence of a discrete articular and retroarticular was a plesiomorphic character of actinopterygians, whereas Patterson & Rosen (1977: 129, character 19) considered an independent retroarticular the derived condition. Yet even if we allow that the articular bone in fossil actinistians is developed from two ossification centres (articular, retroarticular) which may fuse during ontogeny, its single nature in *Polypterus* and Recent amphibians suggests that this is the primitive adult osteichthyan condition.

In placoderms the Meckelian cartilage ossified perichondrally in two regions, as in acanthodians and presumed juvenile *Mimia*. In placoderms and acanthodians the cartilage frequently calcifies, in placoderms invariably as globular calcified cartilage. They are referred to as the mentomandibular and articular ossifications, and are characteristic of many arthrodires (Stensiö 1963a, Miles 1971b) and of *Ctenurella*. Thus two principal ossification centres in Meckel's cartilage, one anterior and one posterior, are probably synapomorphic for a group containing acanthodians, placoderms and osteichthyans, and furthermore these two centres presumably correspond to the hypobranchial and ceratobranchial ossification centres.

2. Dermal bones

The dermal bones of the lower jaw are more numerous in primitive actinopterygians than in later teleosts. The outer surface of the jaw is composed of two dermal bones in *Polypterus*, *Cheirolepis* and *Mimia*. These bones, in sequence the angular and the dentary, are canal-bearing. In many palaeoniscids and primitive neopterygians there is a third bone, the supra-angular, lying dorsal to the angular, sandwiched between it and the back of the dentary. On the inner surface of the jaw there is a further coronoid series, which in *Mimia* and *Moythomasia* comprises a prearticular (double in *Moythomasia*) and four coronoids, and in *Polypterus* a prearticular (= splenial) and two coronoids. A similar dermal bone pattern is encountered in most palaeoniscids (*Pteronisculus*, prearticular, three coronoids), *Ospia*

(prearticular, two coronoids), *Lepisosteus* (prearticular, two coronoids), *Atractosteus* (prearticular, three coronoids) and *Amia* (prearticular, five coronoids). Pearson & Westoll (1979) record a supra-angular in *Cheirolepis* based on a single specimen (RSM 1877.30.5, figs 10b, 11e), but the bone in question is more probably a branchiostegal ray.

Neither a supra-angular nor a coronoid series is present in any living teleost (Nelson 1973); in sturgeons the only dermal ossifications are a prearticular and a dentary whereas in *Polyodon* only the dentary is present. The mandibular canal does not penetrate the dentary in *Polyodon* and is missing altogether in sturgeons.

Coronoids are present in halecomorphs, *Pachycormus*, *Ichthyokentema* and *Pholidophorus higginsii*, but absent in other pholidophorids and in leptolepids (Patterson 1977a). A supra-angular and a prearticular are present in all of these apart from leptolepids other than *Proleptolepis* (Patterson & Rosen 1977: fig. 32A), which retains a supra-angular. Both bones are missing in Recent teleosts. In advanced teleosts the angular and articular bones are co-ossified (Patterson 1977b), but in some leptolepids they fuse during ontogeny, as do the mento-meckelian bone and coronoids of *Mimia* and *Moythmasia*.

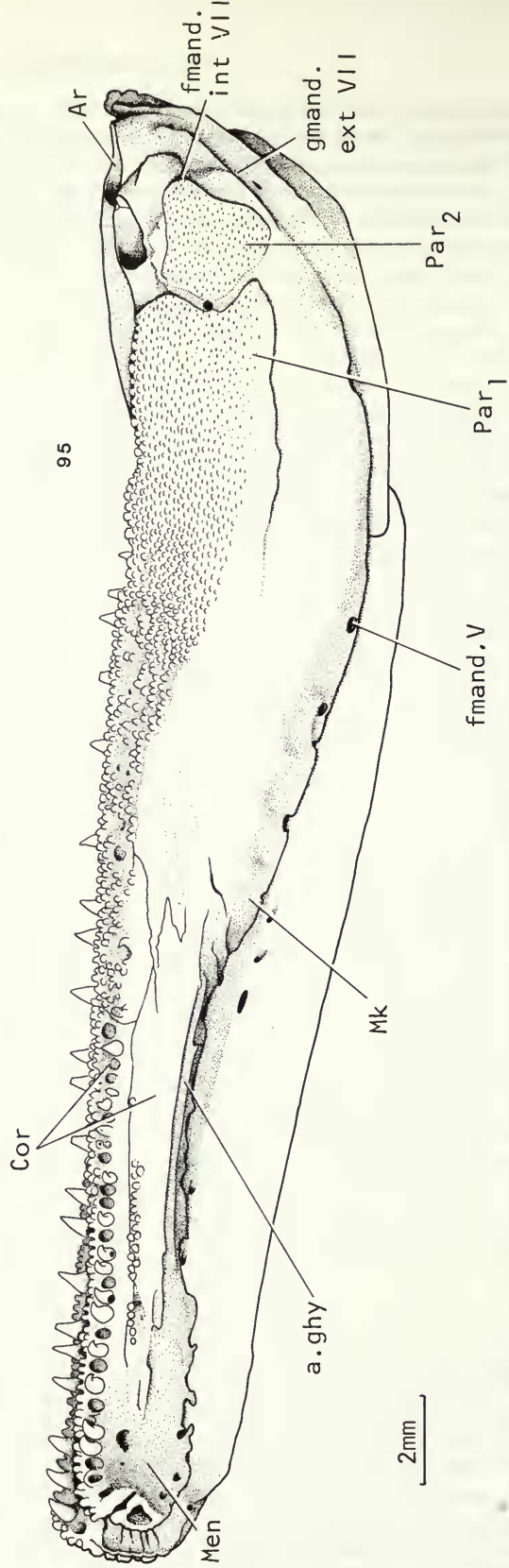
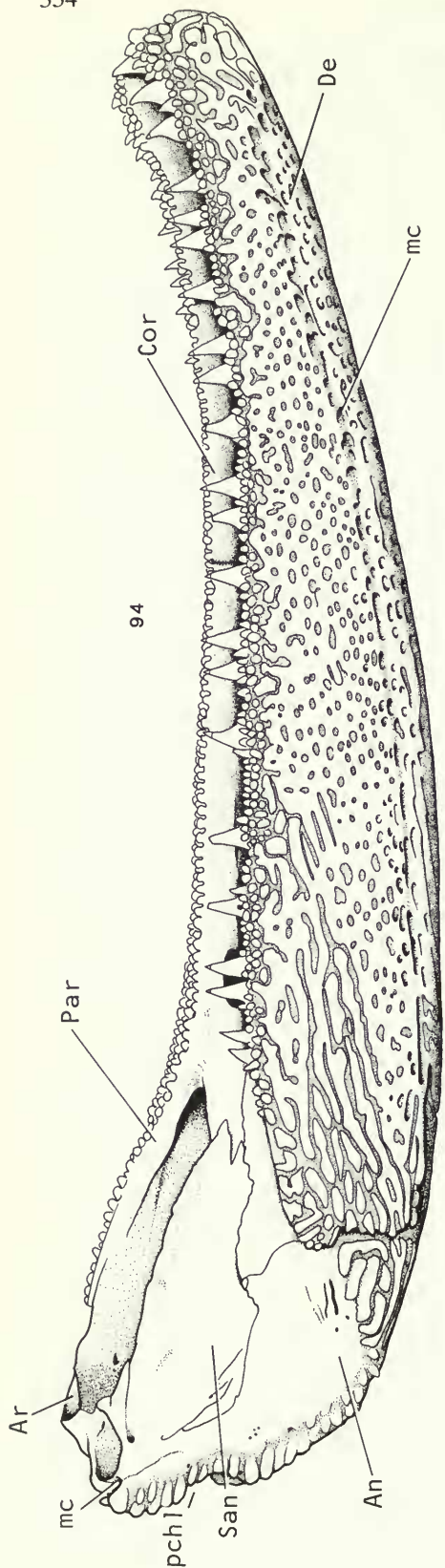
From this analysis I conclude, like Patterson (1982), that the supra-angular has been acquired within the actinopterygians and is primitively absent in *Cheirolepis*, *Polypterus* and *Mimia*.

The presence of a mandibular sensory canal within the dentary bone is unique to actinopterygians (Stensiö 1947). In other osteichthyans this canal runs through an independent splenial series. The splenial series consists of several bones, two in actinistians, four in osteolepiforms, porolepiforms, onychodonts, primitive dipnoans and early tetrapods. The single canal bone (angular) in actinopterygians must be part of this series. The splenial series, from the back forwards, are termed surangular, angular, splenial (postsplenial) and presplenial. The surangular is a canal-bearing bone and is therefore unlikely to be homologous with the actinopterygian supra-angular (Nelson 1973). It carries the mandibular canal and part of the oral canal in osteolepiforms (*Eusthenopteron*, Jarvik 1947) and porolepiforms (*Holoptychius*, Jarvik 1972). In Devonian dipnoans it carries the oral canal and in primitive tetrapods such as temnospondyls (Nilsson 1943, 1944) and anthracosaurs (Panchen 1972, 1977) it is grooved by both the mandibular and oral canals. In actinistians such as *Rhabdoderma* (Forey 1981) and *Latimeria* the posterior bone, which embraces the articular, is called the angular, yet it contains both the mandibular sensory canal and the oral pit-line, much as does the angular in *Mimia* and *Polypterus*. Thus I conclude that the angular of actinopterygians and actinistians is topographically homologous with the surangular of *Eusthenopteron*, *Holoptychius*, dipnoans and tetrapods. Furthermore, the large bone at the back of the lower jaw in later dipnoans (cf. *Neoceratodus*) is better interpreted as a surangular (in the traditional sense) rather than an angular as Thomson & Campbell (1971) and Miles (1977) have regarded it.

In actinistians the large 'angular' is followed by a small splenial and a very small dentary. The dentary, in all but the Devonian forms, bears separate toothplates. There are five coronoids and a large prearticular in *Latimeria*; three of the coronoids lie above the prearticular. In *Macropoma* and *Whiteia* (P. L. Forey, personal communication) there are four coronoids, a large one above the prearticular and three anterior to it. In onychodonts there is a single coronoid with a whorl of teeth much as on the anterior coronoid of *Holoptychius*.

The lower jaws of *Eusthenopteron* and *Holoptychius* (Jarvik 1972) are very similar, and the dentary reaches the articular to form the dorsal margin of the adductor fossa, as in *Cheirolepis*. There are four coronoids, three lying above the prearticular and one anterior to it (parasymphysial plate of Jarvik 1972).

The dipnoan dentary is reduced in size, as in actinistians (Miles 1977: 217) and there is a single median toothplate at the symphysis (adsymphysial plate, Miles 1977). A median adsymphysial plate is an apomorphy of dipnoans. In *Neoceratodus* larvae there is also a separate coronoid on either side of the adsymphysial plate (Semon 1899: pl. 20). The surangular usually forms the margin of the adductor fossa, as in actinistians and tetrapods, and the oral canal passes through the surangular into the dentary in *Chirodipterus*, *Holodipterus* and *Dipnorhynchus*. A full oral line is found in acanthodians, chondrichthyans such as *Chlamydoselachus*, dipnoans and amphibians (Stensiö 1947) and is probably a primitive gnathostome character. But only in



Figs 94-95 *Moythomasia durgaringa* Gardiner & Bartram. Right lower jaw, from BMNH P.53221. Fig. 94, lateral view. Fig. 95, medial view.

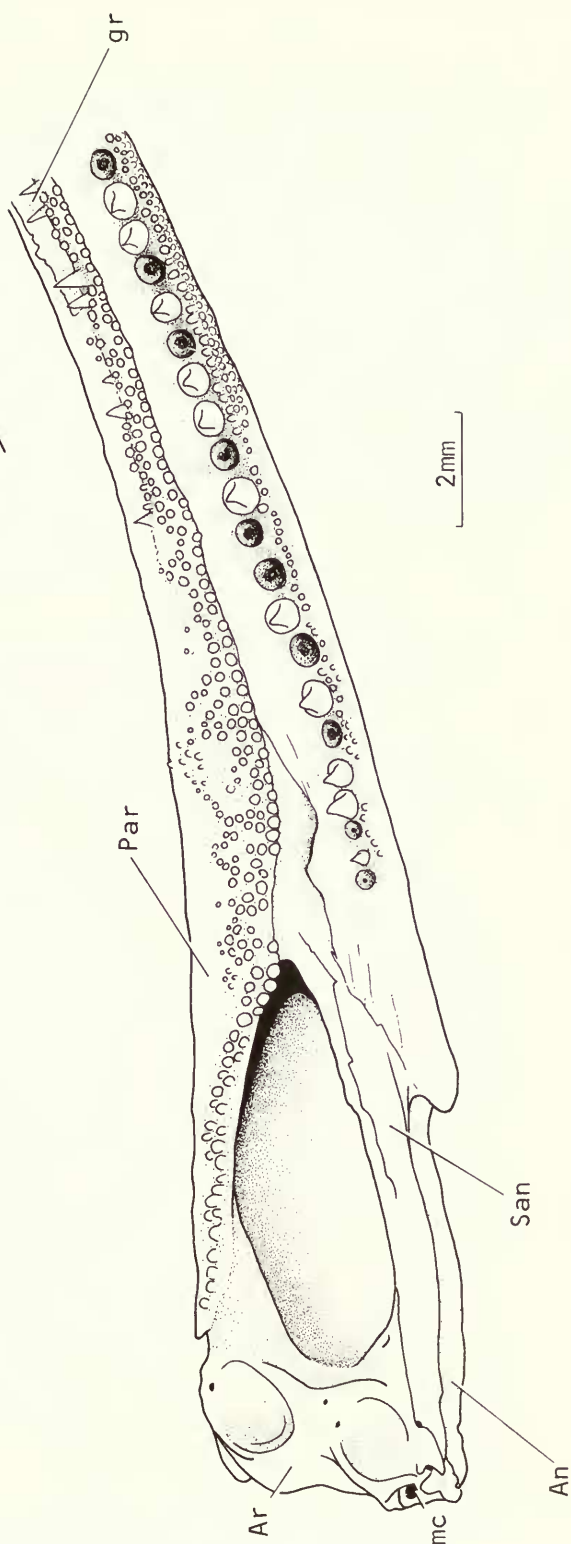
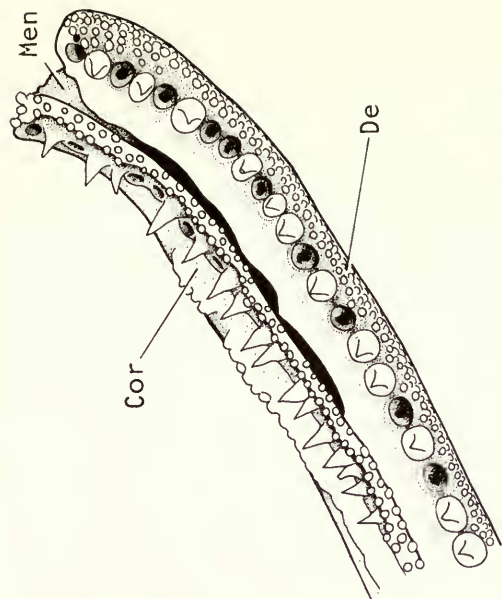


Fig. 96 *Moythomasia durgaringa* Gardiner & Bartram. Right lower jaw in dorsal view, from BMNH P. 53221.

dipnoans and tetrapods (Nilsson 1943, 1944, Panchen 1972) is it ever associated with the dentary. The lower jaws of temnospondyls and anthracosaurs possess three coronoids, but those of Lissamphibia are characterized by the absence of the splenials and angular (= surangular of most authors). The lower jaw of anthracosaurs is characterized by two large meckelian fenestrae, separated by the postsplenial bone.

In acanthodians the ventral margin of Meckel's cartilage frequently sits in a groove along the dorsal margin of the so-called mandibular bone (styliform process of Hancock & Atthey 1869; extramandibular spine of Reis 1890, 1895). The lateral surface of this bone is often ornamented (Miles 1966), confirming its dermal origin. The medial surface of the dentary of *Polypterus* is similarly deeply grooved along its entire length. The mandibular bone stretches the whole length of Meckel's cartilage in *Acanthodes* (and projects anteriorly beyond it in many specimens) but in *Mesacanthus* it is relatively shorter. It has been homologized with the splenials of osteichthyans (Jaekel 1899, Dean 1907) and temnospondyls (Stensiö 1947). A mandibular bone is present in many members of the Diplacanthidae, Ischnacanthidae and Acanthodidae, but its absence in certain Devonian Acanthodidae and the Lower Devonian *Ischnacanthus* has prompted Denison (1979) to consider this the primitive condition. The mandibular canal runs ventral to the mandibular bone; nevertheless from its topographic position, stretching as it does from the articular to the end of the mentomeckelian, it is better homologized with the splenial of osteichthyans than with the dentary. From its distribution with the acanthodians I consider it synapomorphic for a group containing acanthodians and osteichthyans. Both Miles (1971a) and Denison (1979) considered the function of the mandibular bone was to stiffen the Meckelian cartilage.

Teeth when present in acanthodians occur in three forms; as single teeth, spirals or whorls, or fused to dermal jaw bones (Denison 1979). Thus numerous small, single teeth were situated in the lining of the mouth of many ischnacanthids and there was a well-formed, large, lower median symphyseal tooth whorl (cf. *Chlamydoselachus*). Mandibular toothplates are also found in many ischnacanthids and Denison (1979) proposed that these are a unique derived character of Ischnacanthidae. Many attempts have been made to elucidate the structure of these toothplates (Ørvig 1957, 1967a, 1973; Gross 1957; Miles 1966) and it is now generally agreed that they consist of tooth-cusps ankylosed to a supporting bony base. There is no clear boundary between the dentinous tissue of the teeth and the basal bone tissue. The teeth are described as stephanodont (Jaekel 1919) and said to be composed of dentine or dentinous tissue (Ørvig 1973). The underlying bone may be cell-bearing or acellular, fairly dense with vascular canals or cancellous. The teeth are arranged in one or more longitudinal rows and are frequently worn by use. In specimens of *Nostolepis* there are worn tooth-cusps alternating with shearing edges formed by the abraded rows of side-cusps (Ørvig 1973). As in placoderms these worn teeth are never replaced by subsequent teeth in the same positions. The principal tooth-cusps in *Nostolepis* are said to be made up of an external layer of pallial dentine (Gross 1957) or pallial mesodentine (Ørvig 1973). The side cusps of the multicuspidate teeth of *Nostolepis* also consist of mesodentine. The cores of the teeth are of osteodentine and osteomesodentine. Mesodentine is also said to be present in osteostracans (Ørvig 1967a).

In rhenanid placoderms the outer face of the palatoquadrate and Meckelian cartilage is covered by small tesserae with stellate tubercles, in stenioellids by small denticles, and in pseudopetalichthyids by small scale-like plates. Dermal jaw bones are unknown in Acanthothoraci, Petalichthyida and Phyllolepidi, but Ptyctodontida, Arthrodira and Antiarcha have well-developed dermal jaw bones (Denison 1978). In arthrodirids there is a large dermal toothplate or inferognathal associated with the Meckelian cartilage. Anteriorly in *Eastmanosteus* (Gardiner & Miles 1975) the inferognathal sits over the perichondral mentomandibular, but posteriorly it rests on the medial surface of the articular. The inferognathals in brachythoracids carry teeth (Zahntuberkeln of Gross 1957) which are continuous basally with the adjoining bone tissue and may therefore be considered stephanodont as in acanthodians (Jaekel 1919). These teeth are simply cusps on the bone surface which become worn away during life (Miles 1971a). New teeth are said to be added to one end of a tooth row as the gnathals grow at their bases. The teeth consist externally of semidentine surrounding an osteosemidentine

core. In some arthrodires (*Sedowichthys*, *Mylostoma*, Ørvig 1967a, 1973) and the acanthothoracid *Romundina*, the thickened ridges consist of mesodentine, as in many acanthodians. On abraded plates the osteosemidentine is said to have worn away and the biting area to consist of dense bone. The most prominent teeth in arthrodires are seen on the superognathal of the phlyctaeniid *Dicksonosteus*, where they are very markedly tubercular. In antiarchs the inferognathals have a broad biting anterior portion and a slender posterolateral ramus.

In ptyctodonts there is a large crushing or sectorial toothplate. This plate may have a shearing edge, as in *Rhamphodopsis*, or a large central tritural area, as in *Ptyctodus*, or separate tritural cusps as in *Palaeomylus* (Miles 1971a). These toothplates all have dense bone beneath and are strengthened by inwardly-growing hypermineralized columnar tissue (secondary dentine of Gross 1957; osteosemidentine of Ørvig 1973) which in *Ptyctodus* forms the tritural areas as the outer layers of normal dentinal tissue become worn away. A similar columnar tissue is developed in brachythoracid arthrodires, in holocephalans and in dipnoans (Miles 1971a, Ørvig 1973). In arthrodires and ptyctodonts the osteosemidentine is surrounded by semidentine and occasionally by mesodentine. In some ptyctodonts the gnathals have an outer layer of orthodentine and an inner mass of trabecular dentine. In this latter respect and in the similar presumed growth pattern of the stephanodont teeth, placoderms resemble acanthodians

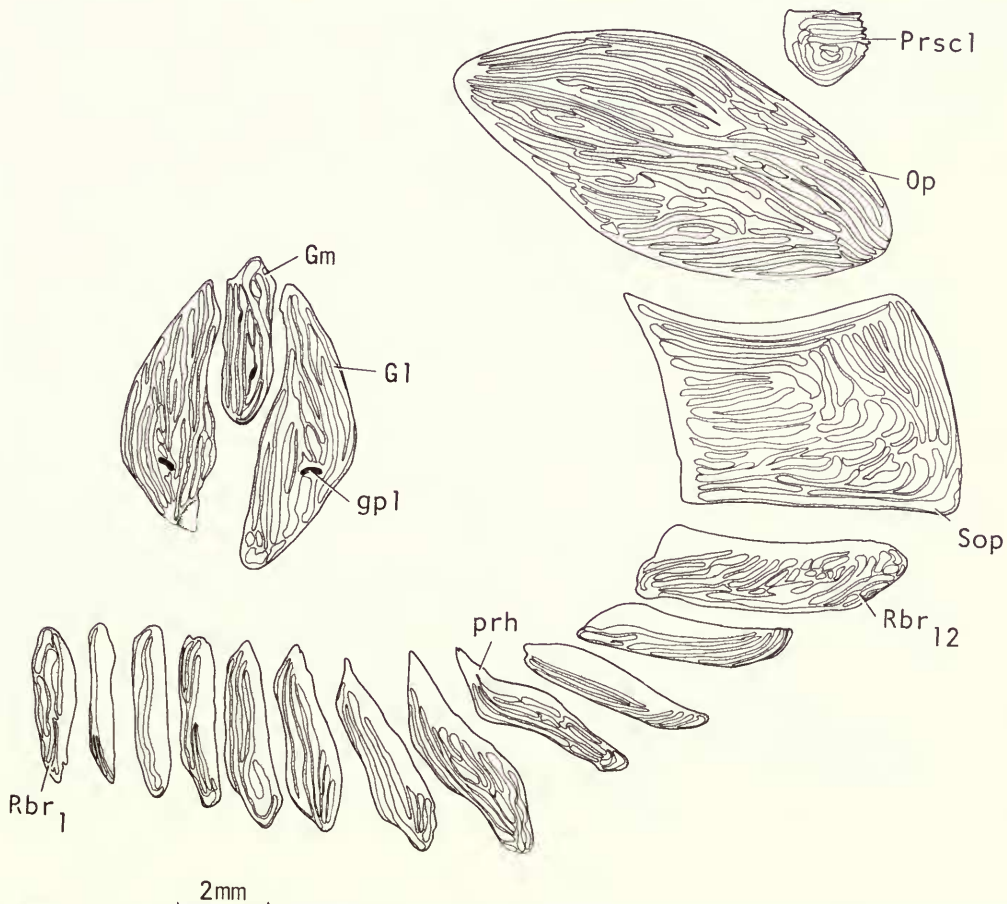


Fig. 97 *Mimia toombsi* Gardiner & Bartram. Opercular, branchiostegal and gular bones and presupracleithrum, drawn as if folded out in one plane, from BMNH P.56495.

(Ørvig 1973). In holocephalans the dermal toothplates arise as whole units in the dermis of the jaws, but in *Neoceratodus* (Kemp 1977) the plates develop from simple groups of isolated cusps which eventually fuse in ridges. All this evidence suggests either that dermal toothplates associated with the dorsal surface of the Meckelian cartilage are a primitive feature of gnathostomes, or that they have been independently developed in holocephalans and in acanthodians, placoderms and osteichthyans. The latter view is the more parsimonious.

The only other dermal bones said to be associated with the lateral and ventral faces of the Meckelian cartilage are the infraprelateral and mandibular plate(s) found in *Bothriolepis* (Stensiö 1931, 1948, Denison 1978). In a specimen of *Bothriolepis* (BMNH P.50898) demonstrated to me by R. S. Miles, the infraprelateral is sutured to the prelateral and is clearly part of the cheek, and the remaining mandibular plate(s) described by Stensiö (1931, 1948) are too incompletely known to comment on.

Operculogular series

Mimia toombsi

The opercular is four-sided with a convex posterior margin. Ventrally it overlaps the dorsal margin of the subopercular. The centre of radiation of the opercular lies in the anterodorsal corner. Internally, just below this centre, there is a small cup-shaped depression (see *Moythomasia*, *dop*, Fig. 99) which as in *Polypterus* (Allis 1922: pl. 11; fig. 33) is presumed to have housed an opercular cartilage.

The subopercular is rectangular and its radiation centre is near the anterior margin. The anterior margin fitted beneath the posterior edge of the preopercular and did not articulate with the hyomandibula as it is said to have done in *Pteronisculus* (Nielsen 1942).

There are twelve branchiostegal rays which diminish in size anteriorly, each ray overlapping the one posterior to it. Several of the branchiostegal rays have a pronounced anterior projection

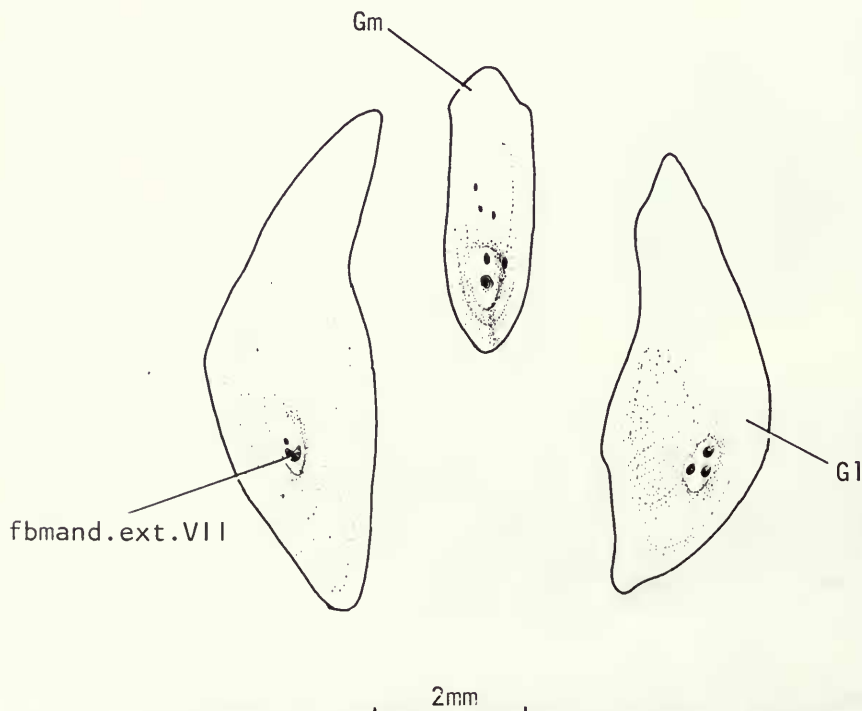


Fig. 98 *Momia toombsi* Gardiner & Bartram. Gular plates in dorsal view, from BMNH P.56495.

(hyoid process) devoid of ornament (prh, Fig. 97), which is also seen in *Cheirolepis* (Pearson & Westoll 1979: 363) and may have been inserted along the ceratohyal as in Recent forms. The first branchiostegal ray, although somewhat larger than the second, neither overlapped nor underlay the lateral gular. The lateral gulars are much larger than the preceding branchiostegal rays. Posteriorly the left lateral gular overlaps the right. The rhombic median gular in turn overlaps the anterior medial edges of the lateral gulars. The radiation centres of the three gulars lie near the centres of the bones, immediately beneath the pit-line; those of the branchiostegals lie much nearer their mandibular margins. Each gular has a slot-shaped pit-line (gpl, Fig. 97) in the form of an arc. On the internal surface there is a corresponding cluster of foramina for branches of the external mandibular nerve (fbmand.ext. VII, Fig. 98). Similar pit-lines are present on the lateral gulars of *Polypterus* (Pehrson 1947, Jarvik 1947) and *Pteronisculus* (Nielsen 1942), and on the median gular of *Amia*.

It will be convenient to deal with the presupracleithrum (Nybelin 1976) at this point. This bone lies behind the posterodorsal corner of the opercular, posterolateral to the supracleithrum. It is overlapped anteriorly by the opercular. In *Polypterus* a similar bone, the posterior postspiracular, overlaps the dorsal edge of the opercular, which is slightly grooved for it. The same bone is present in many palaeoniscids (*Cheirolepis*, *Pteronisculus*, *Boreosomus*) and other fossil actinopterygians, where it has also been called the postspiracular bone (Nielsen 1942: 182). The presence of a presupracleithrum is considered a synapomorphy of actinopterygians.

Moythomasia durgaringa

Moythomasia differs little from *Mimia*. The opercular is more lozenge-shaped and the subopercular is deeper than wide. The median gular is kite-shaped and has a V-shaped pit-line similar to that of *Amia*.

Operculogular series: summary and discussion

1. Branchiostegal rays and gular plates

Numerous long branchiostegal rays are found in many primitive actinopterygians. There are 12 in *Cheirolepis*, *Mimia* and *Moythomasia*, 20 in *Cosmoptychius* and more than 30 in *Tegeolepis*. In *Polypterus* there are no branchiostegal rays and *Polyodon* has only a single pair. *Lepisosteus* has three rays, *Amia* 11 and in higher teleosts there are rarely more than eight. The lateral gulars are in series with the branchiostegal rays and together with the median gular fill the area between the jaw rami. All three gulars occur in the most primitive actinopterygians, including *Cheirolepis*, *Mimia*, *Pteronisculus* and *Haplolepis*. *Boreosomus* has only median gulars (one or two, Nielsen 1942: 349) and *Polypterus* only lateral gulars. Gulars are missing altogether in sturgeons, paddlefishes, *Lepisosteus* and most teleosts, but a median gular is present in *Amia*, pachycormids, pholidophorids, leptolepids, elopids and albulids.

Actinistians (cf. *Diplocercides*, *Rhabdoderma*, *Latimeria*) resemble cladistians in possessing a single pair of lateral gulars and having no branchiostegal rays.

In osteolepiforms, porolepiforms, onychodonts and dipnoans there is an operculogular series with lateral and median gulars as well as a so-called submandibular series. Miles (1977: 258) and Patterson (1982) consider the submandibular series to be a specialization of dipnoans and rhipidistians; Patterson (1982) regards the submandibulars as shortened branchiostegal rays. Jarvik (1963), however, considered them to be part of a mandibular gill-cover and therefore not homologous with branchiostegal rays. Jarvik (1968, 1972) further argued that the primitive gnathostome possessed both series of bones, submandibular and branchiostegal.

In osteolepiforms such as *Eusthenopteron* there are eight submandibular bones with the anterior members of the series intercalated between the gular and the mandible. There are paired lateral gulars and a small median gular similar in size to those in primitive actinopterygians.

In porolepiforms (*Porolepis*, *Glyptolepis*, *Holoptychius*, Jarvik 1972) there are 9–10 submandibulars and very large lateral gulars. The lateral gulars are large in actinistians (*Diplocercides*, *Rhabdoderma*) and cladistians. There may be two median gulars (*Porolepis*) or none (*Holoptychius*). The anterior median gular in *Porolepis* does not carry a pit-line and is best

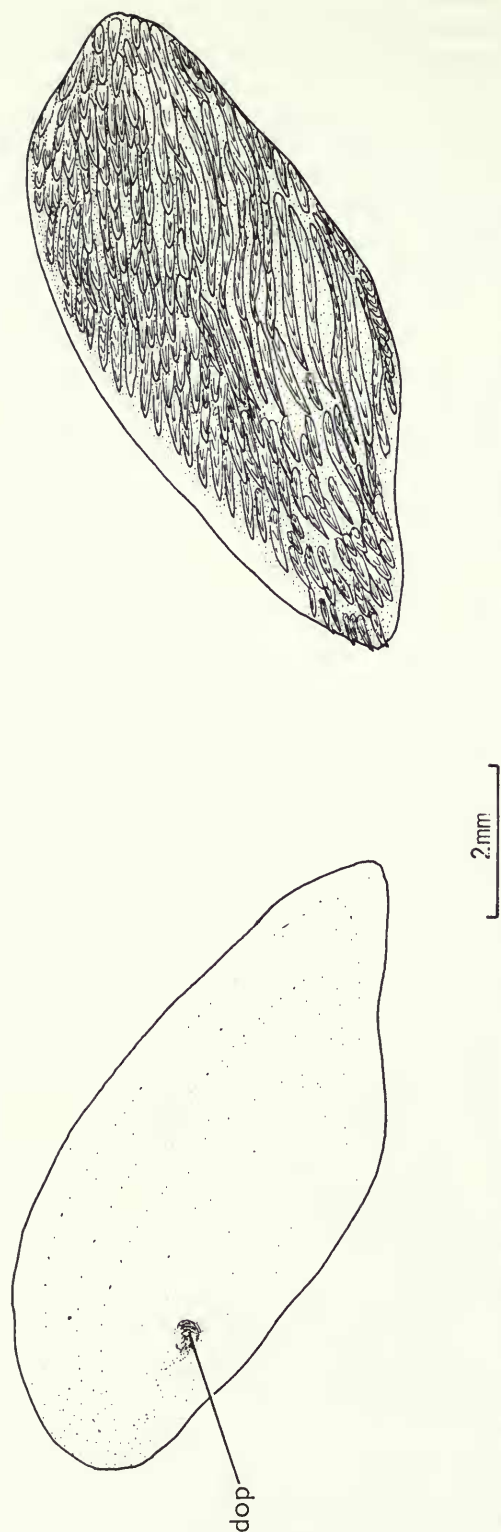


Fig. 99 *Moythomasia durgaringa* Gardiner & Bartram. Right opercular in medial (left) and lateral views, from BMNH P.56480.

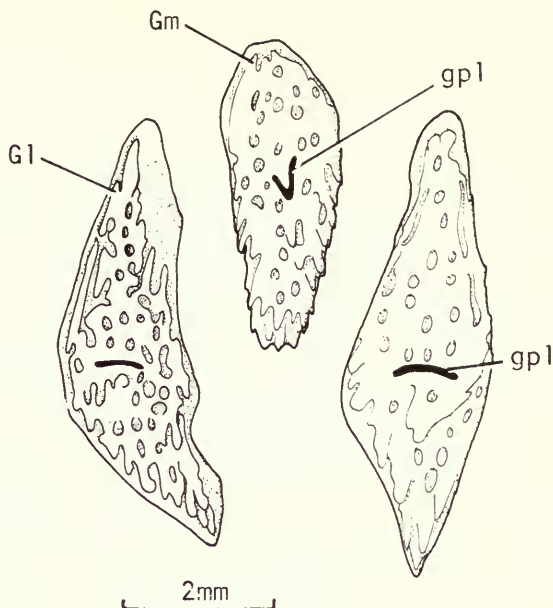


Fig. 100 *Moythomasia durgaringa* Gardiner & Bartram. Gular plates in ventral view, from BMNH P.56480.

homologized with the median submandibular of dipnoans (Jarvik 1967a) and the anterior median gular of *Boreosomus* (Nielsen 1942: fig. 73). The posterior median gular carries a pit-line in both *Porolepis* and *Chirodipterus* (Miles 1977: figs. 105, 129, sbm.m).

In fossil dipnoans the submandibulars vary greatly in size and shape. The most posterior member (subopercular plate 2 of *Griphognathus*, Miles 1977; posterolateral gular of *Scaumenacia*, Jarvik 1967a) looks like a branchiostegal ray, whereas the most anterior (principal submandibular) resembles the lateral gulars. Between them is a short, triangular lateral submandibular (Jarvik 1967a: fig. 5B; Miles 1977: fig. 126). There are usually three submandibulars in dipnoans (*Griphognathus*, *Chirodipterus*, *Scaumenacia*), counting the anterior gular-like pair, but *Rhinodipterus* may have more. If submandibulars are shortened branchiostegal rays then the anterior (principal) submandibulars are more parsimoniously interpreted as anterior lateral gulars and as a synapomorphy of dipnoans. Neither an operculogular series nor branchiostegal rays is present in tetrapods.

In the placoderm *Bothriolepis*, Stensiö (1931, 1948) described a fragmentary series of dermal bones which he suggested were associated with the lower jaw and the hyoid gill cover. These have not been described in any other placoderm; nevertheless Jarvik (1968, 1972) has suggested that some of these elements may belong to the submandibular series. The bones in question do not in my estimation form a recognizable series. Elsewhere in placoderms there is a distinct hyoid gill cover in the form of a dermohyal (submarginal, middle preoperculum, extralateral), which is fused to the head of the hyomandibula in phlyctaeniids (Goujet 1975: fig. 4) and coccosteids (Miles 1971b: fig. 111). The inner surface of the dermohyal is also attached to the opercular cartilage in *Holonema* (Miles 1971b). In some *Pachyosteina* (*Pachyosteus*, *Brachyosteus*) the dermohyal is incorporated into the head shield. A large dermohyal is found in rhenanids (*Gemuendina*, Gross 1963; *Jagorina*, Stensiö 1969), pseudopetalichthyids (*Pseudopetalichthys*, *Paraplesiobatis*, Gross 1962), petalichthyids (*Lunaspis*, Gross 1961) and arthrodires.

The association of the dermohyal with the hyomandibula in placoderms and actinopterygians forces me to regard the dermohyal as a synapomorphy of a group including placoderms and actinopterygians.

In acanthodians, branchiostegal rays are widespread with up to 25 overlapping rays in *Euthacanthus* and *Mesacanthus* (Watson 1937), and 10 or fewer in *Climatius* and

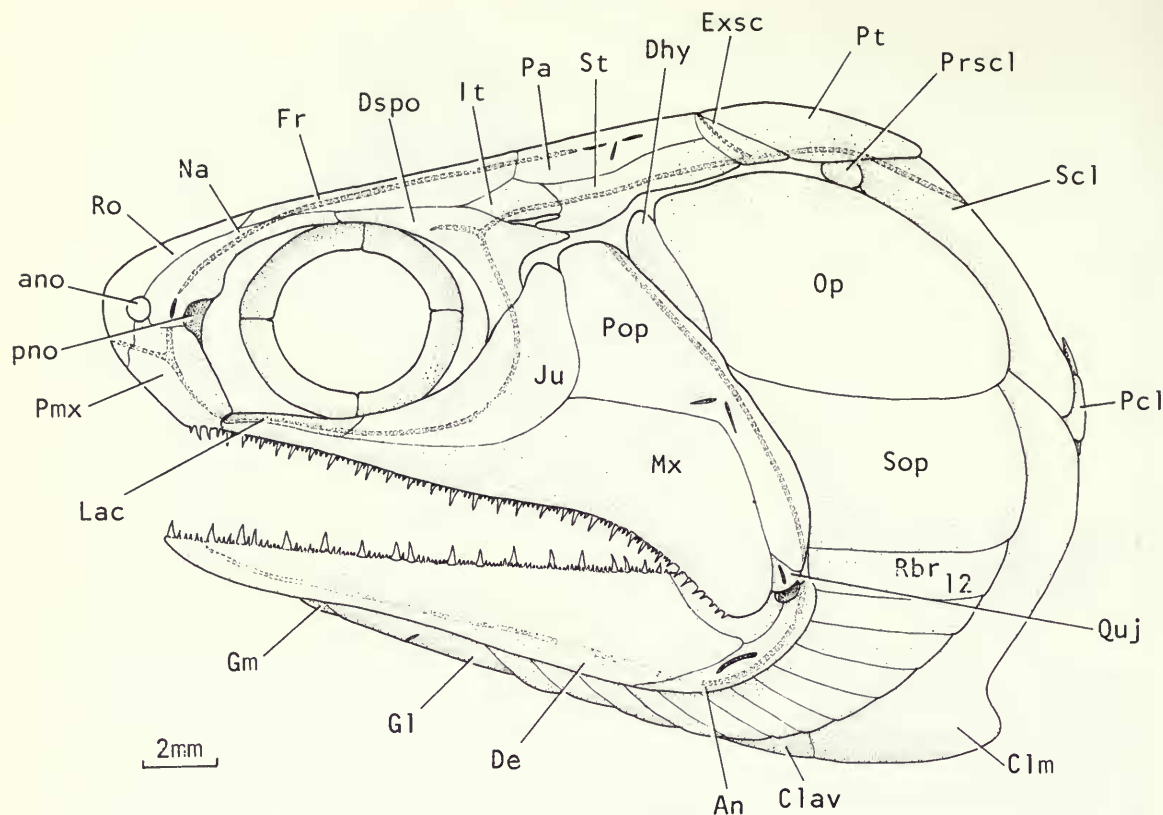


Fig. 101 *Mimia toombsi* Gardiner & Bartram. Restoration of skull in lateral view.

Brachyacanthus. In *Homalacanthus* (Miles 1966) there are some 17 widely-spaced rays behind the 'preopercular' and in *Acanthodes* there are more than 20 very weak rays associated with the ceratohyal (Miles 1973a: pl. 6). In this latter genus they are too short to have covered the gills completely.

In summary, long branchiostegal rays are found in the hyoid operculum of acanthodians and actinopterygians and, as Patterson (1982) has argued, must be synapomorphic for a group containing acanthodians and actinopterygians. The anterior branchiostegal rays are in series with the lateral and median gulars in primitive actinopterygians, and gular plates are considered to be a synapomorphy of osteichthyans. Shortened branchiostegal rays (submandibulars) which have lost all contact with the ceratohyal are regarded as synapomorphic for carcopterygians.

2. Opercular cartilages and opercular bones

An opercular and subopercular are found in almost all non-tetrapod osteichthyans, where they are generally believed to be enlarged branchiostegal rays.

Opercular cartilages are found in chondrichthyans, placoderms and osteichthyans. In selachians there are numerous hyoid ray cartilages and in *Scyllium*, for example, three are associated with the hyomandibula. In chimaeroids a single large opercular cartilage supports the opercular rays. A single large opercular cartilage is also characteristic of such diverse placoderms as *Jagorina*, *Brindabellaspis* and *Bothriolepis*, and in *Holonema* it helps support a dermohyal.

Opercular cartilages are spasmodically distributed throughout actinopterygians. Thus, a small opercular cartilage is seen in larval *Polypterus* and *Anguilla*, and in the adult *Polypterus* it lines the articular facet of the opercular bone as in *Heterotis* and *Elops* (Patterson 1977b: 90). In

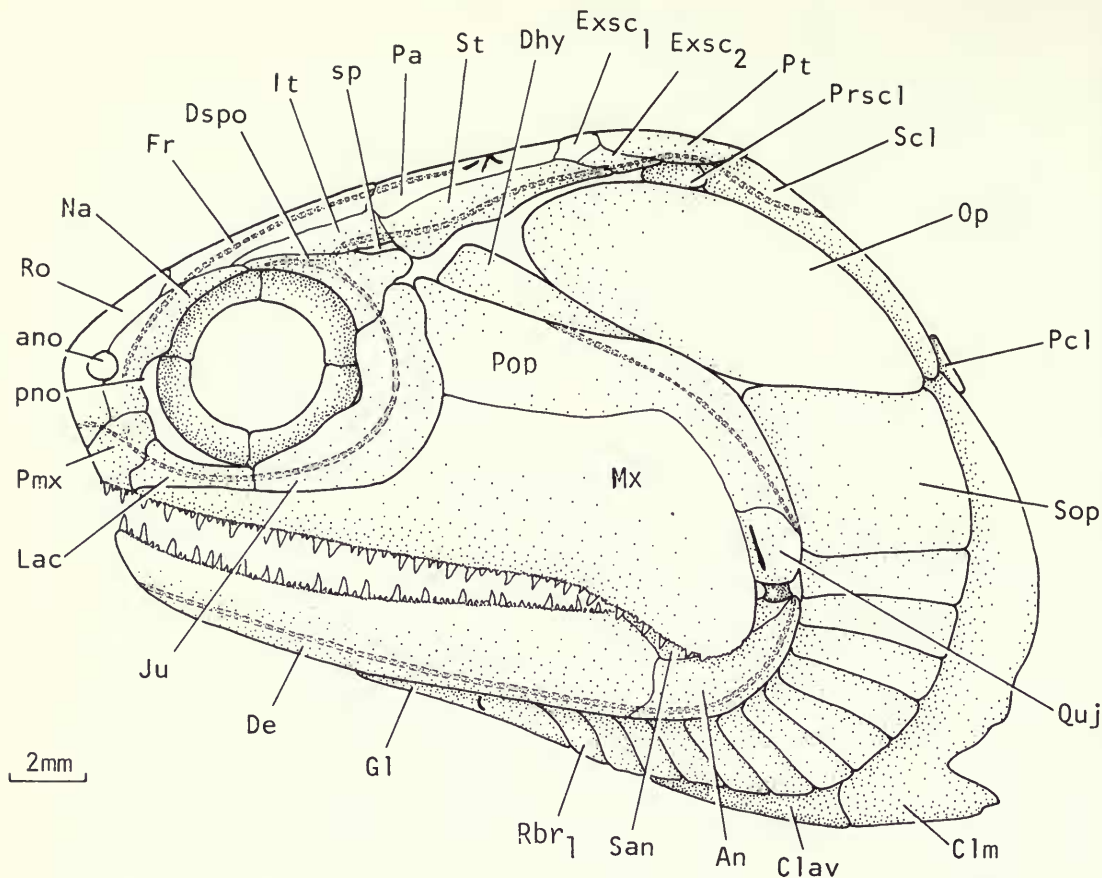


Fig. 103 *Moythomasia durgaringa* Gardiner & Bartram. Restoration of skull in lateral view.

A few primitive actinopterygians also possess accessory operculars in the anteroventral corner of the operculum: these include *Cheirolepis*, *Watsonichthys*, *Cosmoptychius*, *Kentuckia* and *Gonatodus*.

Hyoid and branchial arches

Mimia toombsi

The hyoid arch includes a hyomandibula, dermohyal, interhyal, ceratohyal and hypohyal.

The hyomandibula is a large, stout, gently curved bone which articulates dorsally with the otic region of the neurocranium. Distally it articulates with the interhyal. The hyomandibula is a solid structure of endochondral bone with a small triangular dermohyal intimately fused with its dorsal shank (Pl. 1; Fig. 104). In cross section it is rounded laterally, but medially a well-marked gutter runs across the bottom of the dorsal shank and continues ventrally to the posterior margin. Toothplates clothe the anteromedial surface in front of the gutter, while much smaller plates occur on the anterior margin of the dorsal shank. The disposition of these toothplates is very similar to that described for *Eusthenopteron* by Jarvik (1954: fig. 16A, B). A perichondrally-lined canal (chy, Fig. 104) passes obliquely down through the hyomandibula in the ventrolateral direction. Medially a wide, shallow groove runs down into the mouth of this canal and laterally the canal opens into a shallow groove on the surface of the shaft, just below the dermohyal. This canal presumably transmitted the hyomandibular trunk of the facial nerve, as in *Amia* and *Lepisosteus*. Other surface features of the hyomandibula include a small

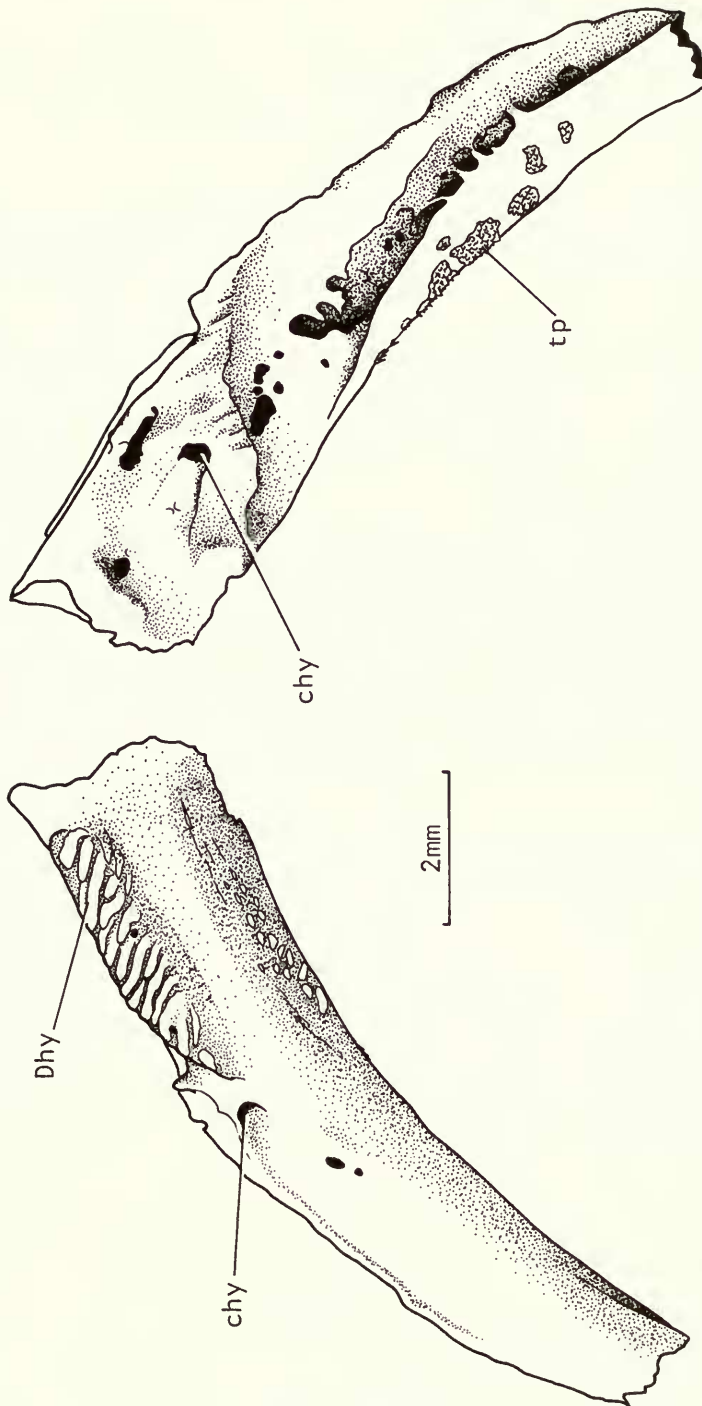


Fig. 104 *Mimia toombsi* Gardiner & Bartram. Right hyomandibula in lateral (left) and medial views, from BMNH P.56498.

projection or notch in the posterior margin near the ventral corner of the dermohyal. This notch may have transmitted the hyoid branch of the facial nerve, as in *Polypterus* (Allis 1922: pl. 17), and as postulated in other palaeoniscids by Stensiö (1925: 169) and in *Eusthenopteron* by Jarvik (1954: fig. 16A, B). However, the condition in *Polypterus* is unique; in all other osteichthyans where the nerve passes through the bone (*Amia*, *Lepisosteus*, generalized teleosts, *Latimeria*, larval *Neoceratodus*) it never divides into the mandibular and hyoid branches until it has pierced the hyomandibula (see also *Moythomasia*, Fig. 105). It therefore seems unlikely that it divided into its constituent branches prior to its passage through the hyomandibula in either *Mimia* or *Eusthenopteron*.

Both the interhyal and ceratohyal are perichondral shells lacking any endochondral ossification. The interhyal is a small, somewhat cylindrical bone, open at each end where it articulated with the lateral portion of the proximal end of the ceratohyal and the distal end of the hyomandibula (Fig. 108), much as in *Polypterus*. It does not articulate with either the palatoquadrate or the Meckelian cartilage, as it is said to do in *Pteronisculus* (Nielsen 1942: 175; fig. 42).

The ceratohyal is a stout, flat, slightly curved bone, expanded ventrally in its posterior third. On its lateral face there is a broad longitudinal groove (see *Moythomasia*, ahy, Fig. 106) for the afferent hyoidean artery. A similar groove has been reported in *Pteronisculus*, *Australosomus* (Nielsen 1949: fig. 37), *Plegmolepis*, *Pygopterus* (Aldinger 1937: figs 19, 41B) and *Eusthenopteron* (Jarvik 1954: 22; fig. 8A). A continuous toothplate runs along its dorsomedial margin (BMNH P.53245), as in *Elops*.

The hypohyal, like the ceratohyal, is a perichondral ossification, open at both ends. It is a flat, strongly curved bone which lies in the vertical plane, with its distal edge directed posteromedially to articulate with the anterior end of the basibranchial. A few small toothplates are found on the dorsomedial surface (Fig. 107). A stout ventral projection of the hypohyal presumably served for the insertion of the sternohyoideus muscle (cf. *Polypterus*, *Lepisosteus*).

Five branchial arches are present, each component of which consists of perichondral ossifications with a weak endochondral core. The individual ossifications are presumed to have articulated with one another by cartilaginous epiphyses. The elements are usually scattered, but there are enough specimens with parts of the arches in position to enable precise reconstructions to be made.

The first branchial arch consists of hypobranchial, ceratobranchial, epibranchial, infrapharyngobranchial and suprapharyngobranchial. The hypobranchial is a long, slender bone with an enlarged, inturned distal end which articulates with the anterior end of the basibranchial, immediately behind the hypohyal (Fig. 108). Thus the first hypobranchial and hypohyal share the same articular facet, as they do in *Pteronisculus* (Nielsen 1942: fig. 45) and *Australosomus* (Nielsen 1949: 121), and as they partly do in *Polypterus* (Allis 1922: pl. 8). Ceratobranchial 1 (Fig. 108) is a very long rod, strongly arched dorsoventrally. It is semicircular in section, with a deep, longitudinal groove on its ventral face (see *Moythomasia*, Fig. 115). The groove is presumed to have carried the afferent artery and branchial nerve, as in *Polypterus*, *Amia* etc. Proximally the edges of the ceratobranchial groove have closed up to form a foramen for the artery and nerve as in *Moythomasia* (fcb, Fig. 115). A similar foramen has been described in the Gogo dipnoan *Griphognathus* (Miles 1977: fig. 135). Two rows of toothplates cover the dorsomedial surface of both the hypobranchial and ceratobranchial. The ventromedial edge of the ceratobranchial is often regularly scalloped. The first epibranchial is about half the length of the ceratobranchial and has a deep longitudinal arterial groove in its posterior margin. Ventrally the lateral wall of the groove is produced posteriorly to form a partially covered canal. Dorsally the medial wall is developed as a dorsally-directed process for the articulation of suprapharyngobranchial 1. Toothplates clothe the lateral edge of the epibranchial and appear to be arranged in at least two rows (Fig. 116B). The first infrapharyngobranchial is a short, elbowed bone, which articulates with the anteriorly-directed proximal end of epibranchial 1 and with a ventral facet on the otic portion of the neurocranium. Ventrally it is covered by a row of small toothplates. The first suprapharyngobranchial is a flat bone, considerably larger than the infrapharyngobranchial. Posteroventrally it has a short process projecting beyond the articular

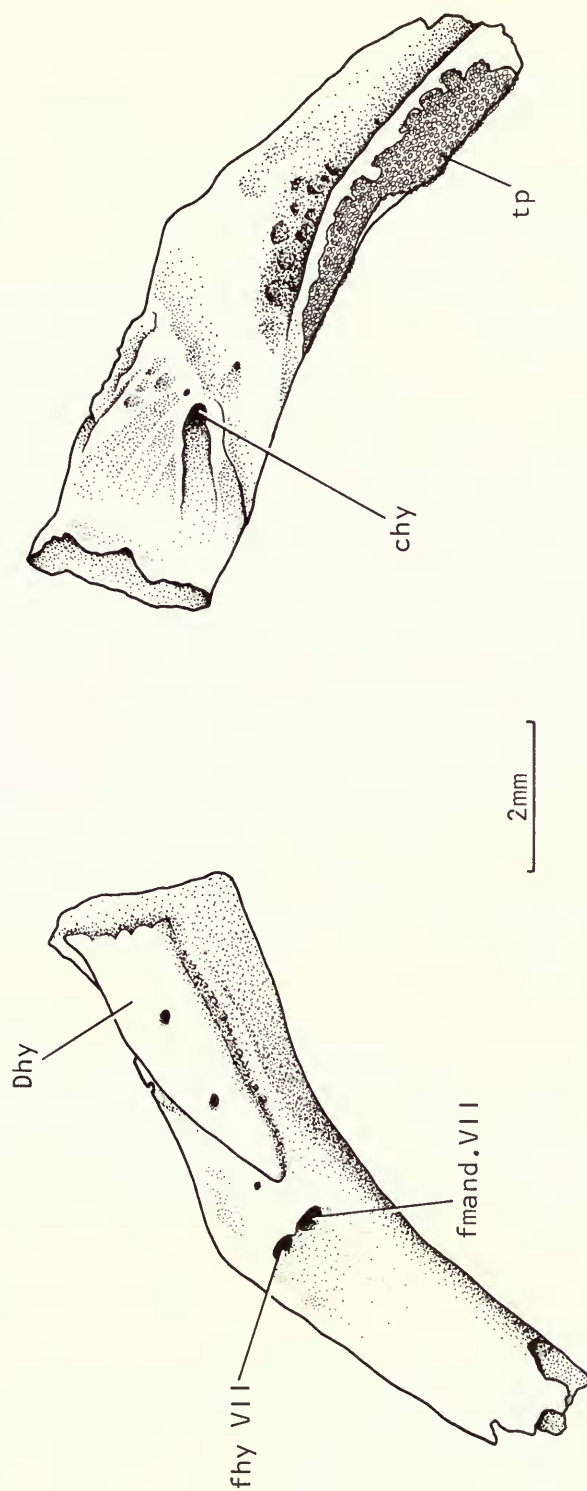


Fig. 105 *Moythomasia durgaringa* Gardiner & Bartram. Right hyomandibula in lateral (right) and medial views, from BMNH P.53255.

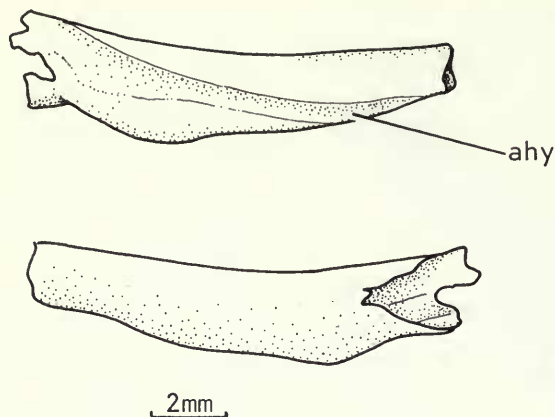


Fig. 106 *Moythomasia durgaringa* Gardiner & Bartram. Right ceratohyal in lateral (above) and medial views, from BMNH P.56475.

facet. Its medial face is slightly concave where it fitted against the lateral face of the otic region of the neurocranium, above the vestibular fontanelle and jugular canal and anterior to the exit of the vagus nerve, as in *Pteronisculus* (Nielsen 1942: fig. 47). In *Acipenser* the first suprapharyngobranchial articulates below the jugular vein, but the second articulates above it (Bertmar 1959: 305).

The second hypobranchial (Figs 111, 113) is stouter and a little longer than the first. Its distal end is broad and the articulatory facet directed dorsally. It articulated about one-third of the way along the basibranchial by a nearly vertical facet. Toothplates clothe the dorsal surface of the shank behind the expanded distal head. The second ceratobranchial is similar to the first, but epibranchial 2 is two-thirds of the length of epibranchial 1. Infrapharyngobranchial 2 is a little smaller than the first but is similarly shaped, with articular facets at either end and small toothplates ventrally. No articular facet for its anterior end has been observed on the braincase,

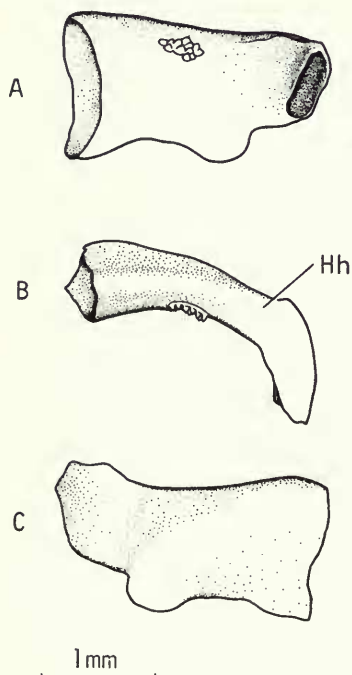


Fig. 107 *Mimia toombsi* Gardiner & Bartram. Left hypohyal in (A) medial, (B) dorsal and (C) lateral views.

but by comparison with *Acipenser* it is likely that it articulated with the ventral margin of the occiput. The second suprapharyngobranchial is a smaller version of the first. It is presumed to have articulated with (or pressed against) the occipital region, as in *Acipenser*.

The third arch has a very short hypobranchial and epibranchial and does not contain either a supra- or infrapharyngobranchial. The head of the hypobranchial is tapered and inturned where it articulated with an oblique facet on the basibranchial. Ventrally it has a process similar to that on the hypohyal, except that it lacks a perichondral covering. The third ceratobranchial is the same length and shape as the second, whereas the third epibranchial is about two-thirds the length of the second and has a characteristic broad flange projecting back from its posteromedial edge. A distinct notch in the ventral margin of this flange gives a beaked appearance to the posteroventral edge. Toothplates are confined to the lateral edge of the epibranchial.

The fourth arch, like that of *Eusthenopteron*, lacks an ossified epibranchial. This may be missing altogether, or may have been cartilaginous, as in *Latimeria*. (I erroneously attributed both a third infrapharyngobranchial and a fourth epibranchial to *Mimia*; Gardiner 1973: fig. 9). The fourth hypobranchial (Figs 111, 112) is a short, squat ossification, shorter than the third hypobranchial, which articulated by way of a broad horizontal facet with the extreme hind end of the basibranchial. The fourth ceratobranchial differs from the third only in being somewhat shorter.

The fifth branchial arch is only represented by a ceratobranchial which is a very slender ossification, circular in cross-section and devoid of a longitudinal groove.

The basibranchial is a sturdy ossification, very similar in shape to that of *Polypterus*. The entire anterior end forms an articular facet for the hypohyals and first hypobranchials. There are three other oval facets for the remaining hypobranchials: that for hypobranchial 2 is almost vertical, that for hypobranchial 3 more oblique, and the facet for hypobranchial 4 is horizontal. The basibranchial is thickened dorsoventrally in the plane of the long axes of the facets for the second and third hypobranchials, and is also produced ventrally beneath the facets for the fourth. The dorsal surface is flat and supports a series of irregularly-arranged toothplates similar to those on the epibranchials.

Although the basibranchial is frequently a single ossification there is a clear evidence of three ossification centres in several specimens. Thus in BMNH P.53237 there are two separate ossifications with the junction between them lying behind the articulation of the third hypobranchial. The same specimen also shows a break in the perichondral covering behind the articulation facet for the second hypobranchial and this marks the junction of the first two ossification centres.

Moythomasia durgaringa

The hyomandibula of *Moythomasia* is more distinctly elbowed than that of *Mimia* and the canal for the hyomandibular trunk of the facial nerve divides as it passes obliquely down through the hyomandibula, to open by two foramina on the lateral surface of the shaft below the dermohyal. The more anterior foramen is thought to have transmitted the mandibular branch, while the posterior served for the passage of the hyoid branch (fhy.VII, Fig. 105). The remainder of the hyoid arch, the branchial arches and basibranchial agree with the corresponding structures in *Mimia*.

Hyoid and branchial arches: discussion

1. Hyoid arch

The hyomandibula is a clearly recognizable element in most gnathostomes and in osteichthyans where it ossifies it does so as a single bone. Most authors have agreed that it represents the epihyal in sharks (Luther 1909, Allis 1915, de Beer 1937), but some workers (Gegenbaur 1872, Holmgren 1940) have suggested that it incorporates pharyngohyal and epihyal elements; Holmgren (1943) and Jarvik (1977) proposed that in selachians, in addition to the pharyngoepihyal, there was also a ventral component from a mandibular ray. Holmgren's evidence (1940, 1943) for both selachians and actinopterygians was based on embryological

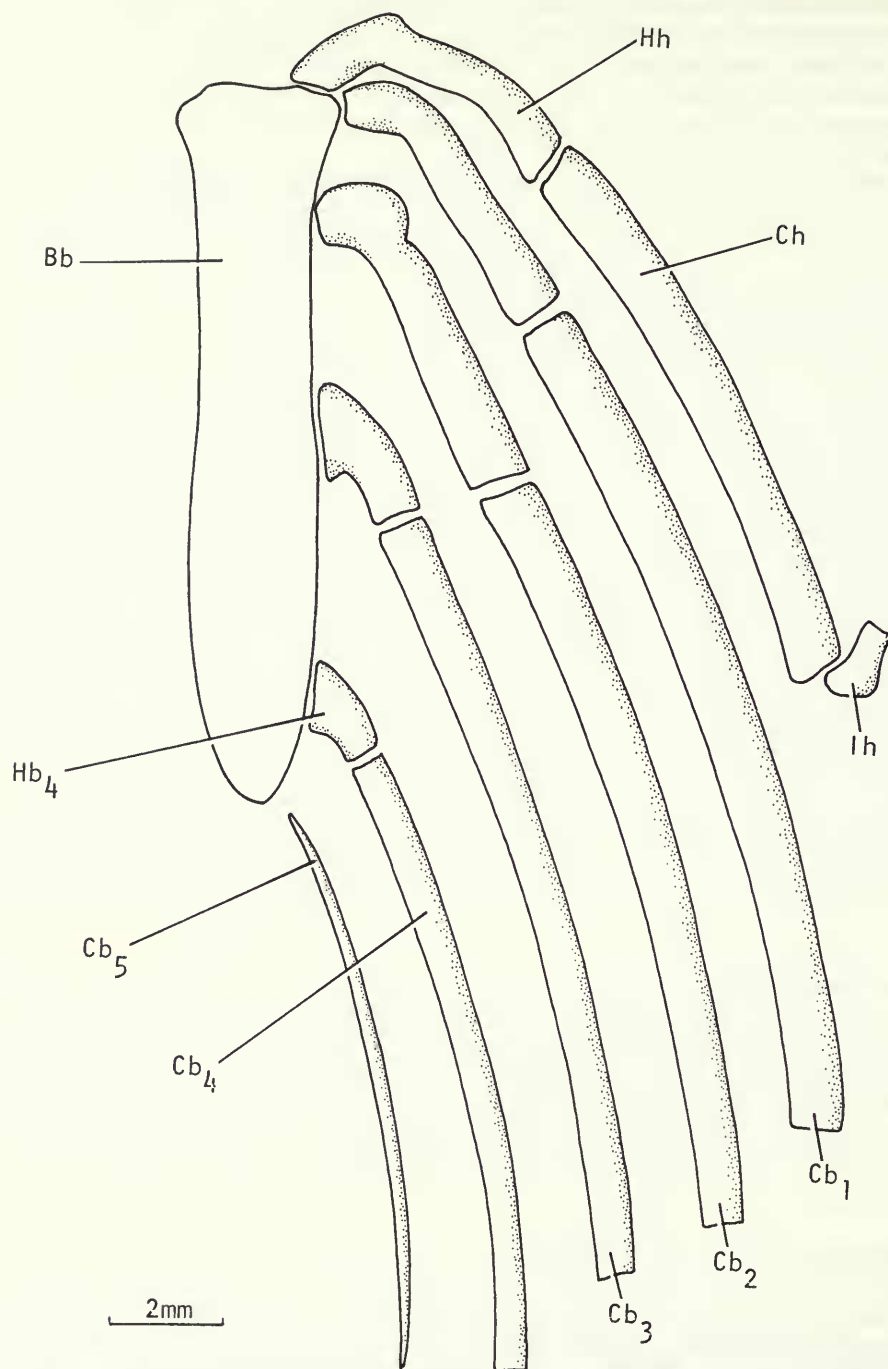


Fig. 108 *Mimia toombsi* Gardiner & Bartram. Restoration of ventral gill-arch elements in dorsal view. Paired elements shown on right side only.

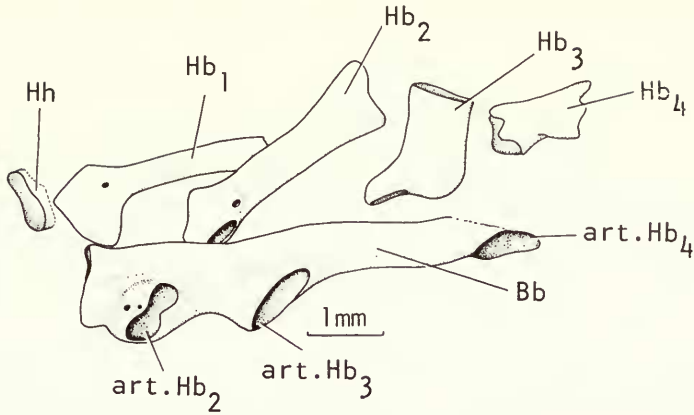


Fig. 109 *Moythomasia durgaringa* Gardiner & Bartram. Basibranchial and hypobranchials of the right side, from BMNH P.51380.

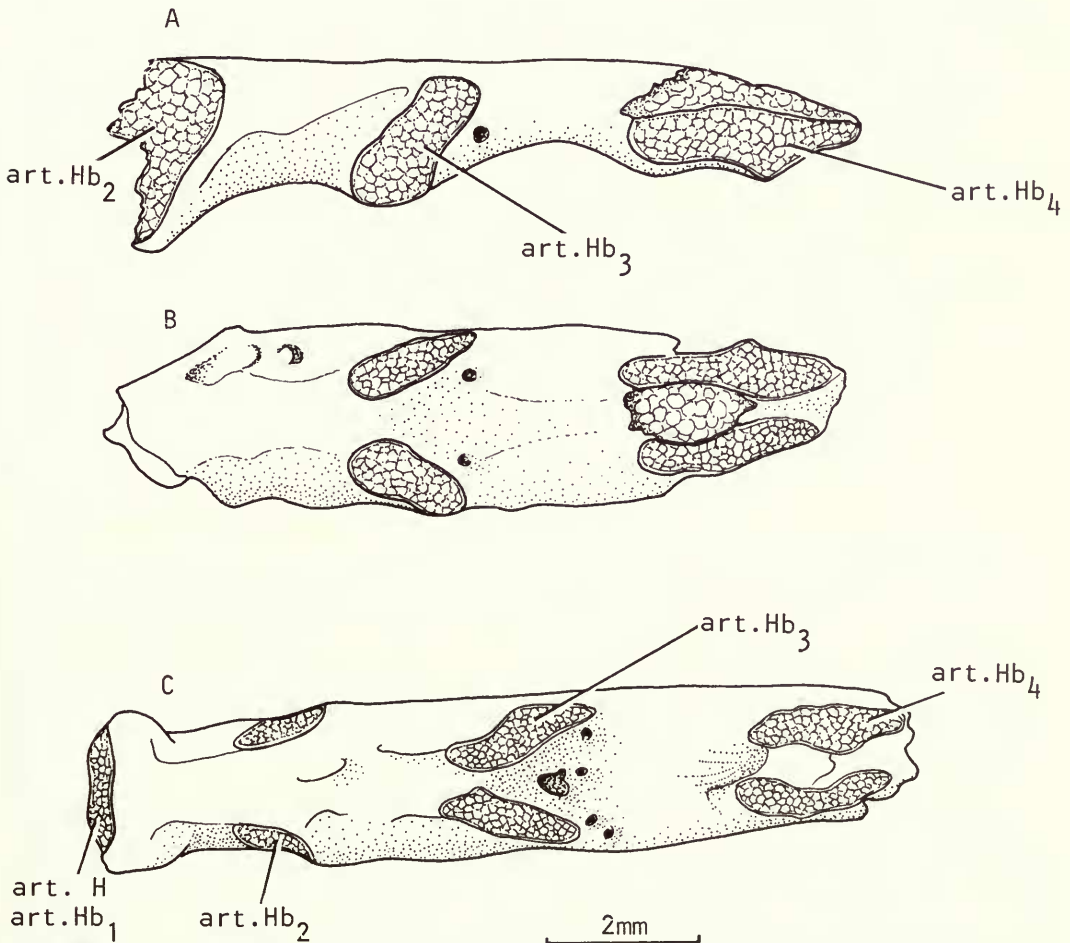


Fig. 110 *Moythomasia durgaringa* Gardiner & Bartram. Basibranchial in (A), lateral and (B), ventral views, from BMNH P.53221. (C), basibranchial in ventral view from Western Australian Museum no. 20.4.244 (holotype).

stages prior to chondrification and his observed blastematic rudiments were merely mesenchymatous cell masses. Moreover his observations lead to unacceptable conclusions, such as the inference that the composition of the upper end of the hyomandibula differs in sharks and most actinopterygians from that in rays and *Acipenser*!

The presence of the interhyal in osteichthyans and of a ceratohyal ossified in two sections in neopterygians has further complicated the problem. Thus Allis (1915) believed that the hyomandibula in teleosts was essentially a pharyngohyal and the interhyal the epihyal element, while the posterior ceratohyal in neopterygians is often called an epihyal. In *Acanthodes* (Reis 1896, Miles 1964) the hyomandibula is perichondrally ossified in two sections. Miles (1964) has compared the dorsal and ventral ossifications respectively with the laterohyal and epihyal of osteichthyans, whereas Nelson (1968) regarded the dorsal element as the pharyngohyal. However, the two ossifications of the hyomandibula of *Acanthodes* are clearly in the same cartilage and this is consonant with the structure of acanthodian epibranchials which also ossify from dorsal and ventral centres (Miles 1973a: 93). The two ossifications of the hyomandibula of acanthodians are considered a synapomorphy of that group (compare for example the single perichondral ossification of the hyomandibula of *Jagorina*, *Coccosteus* and *Dicksonosteus*).

In *Neoceratodus* the cartilaginous hyomandibula is said to exhibit great variability (Ridewood 1894: 637), but if we disregard the chondrification in the hyosuspensory ligament, there are two chondrifications (Bertmar 1959, Fox 1965). The more dorsal is the hyomandibula, and the ventral the interhyal. In Devonian dipnoans these ossify separately (Miles 1977).

Finally, the hyomandibula of recent holocephalans is unique in being non-suspensory and in possessing an additional cartilage dorsally, called the pharyngohyal (Devillers 1958: 584). I consider this latter element to be a new formation and do not agree with de Beer & Moy-Thomas (1935) that the holocephalans are the only living fishes with a complete hyoid arch. A pharyngohyal is therefore regarded as an autapomorphy.

An unusual feature of the hyomandibula of *Polypterus*, many palaeoniscids and some placoderms (see p. 341) is the presence of a dermohyal. This bone, firmly bound to the dorsolateral corner, has generally been regarded as an accessory hyomandibula in actinopterygians (van Wijhe 1882, Bridge 1888) and to be serially homologous with the spiracular ossicles of *Polypterus*. Despite its obvious dermal ornamentation the dermohyal of *Polypterus* has a complex ontogenetic history. Allis (1922) said that during development it contained a piece of cartilage and he therefore regarded it as a transformed hyal ray, a view supported by Holmgren (1943) and Bertmar (1959). Holmgren (1943: fig. 45) and Daget (1950) showed that the dermohyal first appears as a perichondral bone, with Holmgren (1943: 95) adding that the subsequent bone lamella could easily be mistaken for dermal bone. I conclude that the dermohyal is a dermal element fused with the head of the hyomandibula and synapomorphous for actinopterygians and placoderms.

A peculiar feature of the hyomandibula of *Polypterus*, advanced palaeoniscids and other actinopterygians is an opercular process. Although it is possible to regard the posterodorsal angle of the expanded region of the hyomandibula of *Nesides*, *Latimeria* and *Griphognathus*, and the posterior corner of the elbow in *Megalichthys*, as incipient opercular processes, only in actinopterygians is this process distinct. This, however, did not prevent Jarvik (1954: 32) from postulating the presence of a cartilaginous opercular process on the posteroventral margin of the hyomandibula of *Eusthenopteron*. The formation of the process itself has also caused considerable speculation; Allis (1915) for example thought it was a hyoid ray fused on to the hyomandibula, but his view was criticized by Edgeworth (1926) on the grounds that he (Allis) had not demonstrated the existence of separate cartilaginous primordia. Holmgren (1943: 86), on the other hand, maintained that the hyomandibula of *Amia* (and *Salmo*) resulted from the fusion of two blastematic rudiments, the epihyal and suprapharyngohyal (= opercular process). But these rudiments coalesce prior to chondrification and Edgeworth's criticism of Allis equally applies to Holmgren's (1940, 1943) work. In *Polypterus* the opercular process may be related to the possession of protractor hyomandibularis and dilatator opercularis muscles and in actinopterygians to the dilatator opercularis. Apart from *Polypterus* an opercular process is found in *Boreosomus*, *Acrorhabdus*, *Lepisosteus* and halecostomes. An opercular process is not found

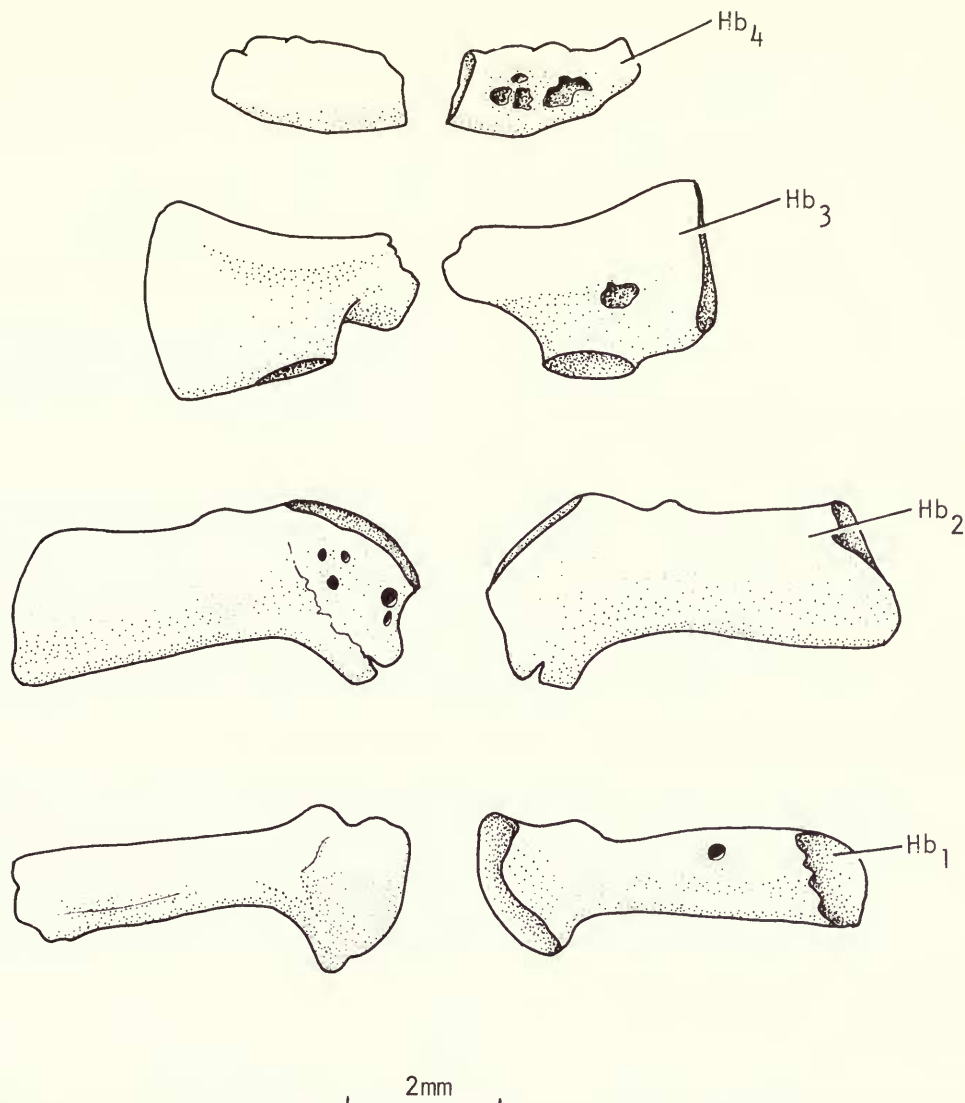


Fig. 111 *Moythomasia durgaringa* Gardiner & Bartram. Right hypobranchials in lateral (left) and medial views, from BMNH P.53256.

in *Cheirolepis*, *Mimia*, sturgeons and many palaeoniscids (*Elonichthys*, *Cheirodus*, etc.). From this evidence, and if our phylogeny is correct (Rosen *et al.* 1981, Patterson 1982), I conclude that the opercular process has arisen on at least two occasions, once in *Polypterus* and once within the actinopteryans.

The hyomandibular trunk of the facial nerve passes medial to the hyomandibula in actinopterygians and turns outwards either to pass round in front of it, as in *Polypterus*, behind it as in *Acipenser* and *Polyodon*, or to penetrate the bone as in palaeoniscids and most actinopteryans. In adult *Acipenser fluvescens* the hyomandibular nerve passes through a cartilaginous extension of the hyomandibula (Jollie 1980). Except in *Polypterus* the hyomandibular nerve does not divide into its mandibular and hyoid branches until it has penetrated or passed the hyomandibula. In *Polypterus* it branches prior to crossing the hyomandibula, the mandibular branch passing round the anterior face and the hyoid branch

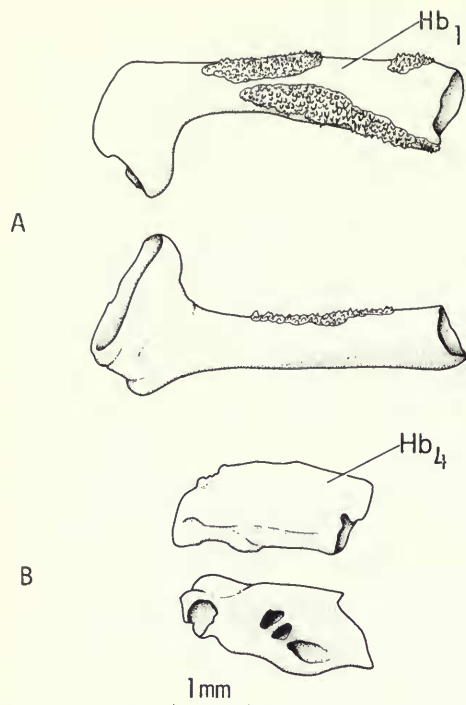


Fig. 112 *Mimia toombsi* Gardiner & Bartram. (A), right first hypobranchial in dorsal (above) and ventral views; (B), right fourth hypobranchial in dorsal (above) and lateral views; all from P.56498.

behind the posterior face, above the opercular process. The relationship of the mandibular branch in *Polypterus* is unique. In *Cheirolepis* there is no nerve foramen and the hyomandibular nerve is thought to have passed round behind the hyomandibula, as in *Acipenser*. In *Eusthenopteron*, *Ectosteorhachis* (Romer 1937) and *Porolepis* (Jarvik 1972) the hyomandibular nerve pierced the hyomandibula, as in most actinopterans. In *Latimeria* (Millot & Anthony 1958: fig. 20) and *Nesides* (Bjerring 1977: fig. 25) the mandibular and hyoid branches fork after

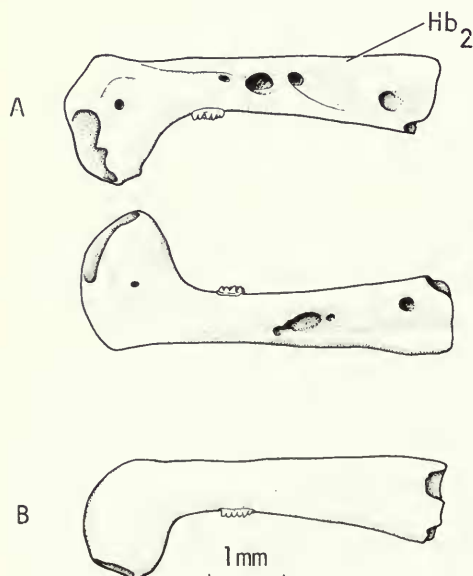
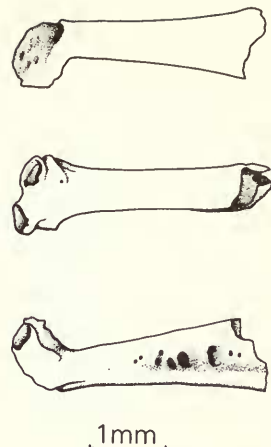


Fig. 113 *Mimia toombsi* Gardiner & Bartram. (A), second hypobranchials in ventral view; (B), right second hypobranchial in dorsal view; both from BMNH P.56498.

Fig. 114 *Moythomasia durgaringa* Gardiner & Bartram. Right first hypobranchial in dorsal (top), lateral (centre) and ventral (bottom) views, from BMNH P.53255.



penetrating the hyomandibula, much as in *Moythomasia*, and the hyoid branch then passes through a further small bridge of cartilage or bone before leaving the posterior margin. The hyomandibular nerve likewise passed through the hyomandibula in the fossil dipnoans *Griphognathus* and *Chirodipterus* (Miles 1977), but in *Neoceratodus* it passes anterior to it, as in selachians, before dividing into the hyoid and mandibular branches. In larval *Neoceratodus* (Bertmar 1963), in contrast, it passes through the hyomandibula.

There is no nerve foramen in the hyomandibula of placoderms (*Jagorina*, *Coccosteus*,

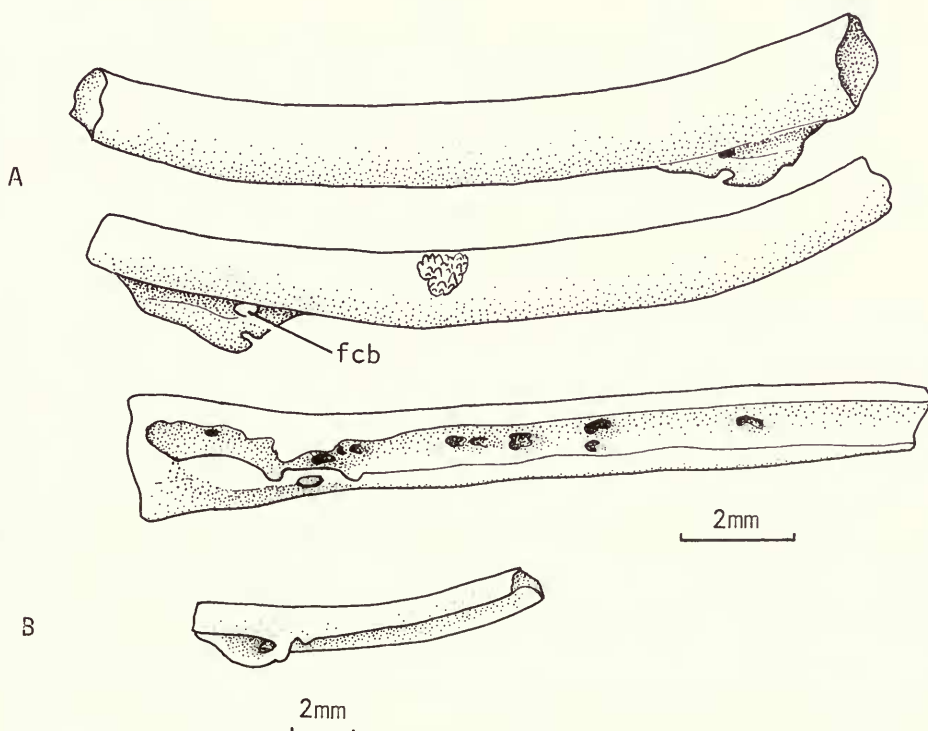


Fig. 115 *Moythomasia durgaringa* Gardiner & Bartram. (A), first left ceratobranchial in lateral, medial (centre) and ventral views, from BMNH P.53218. (B), posterior end of first right ceratobranchial in ventrolateral view, from Western Australian Museum no. 20.4.244 (holotype).

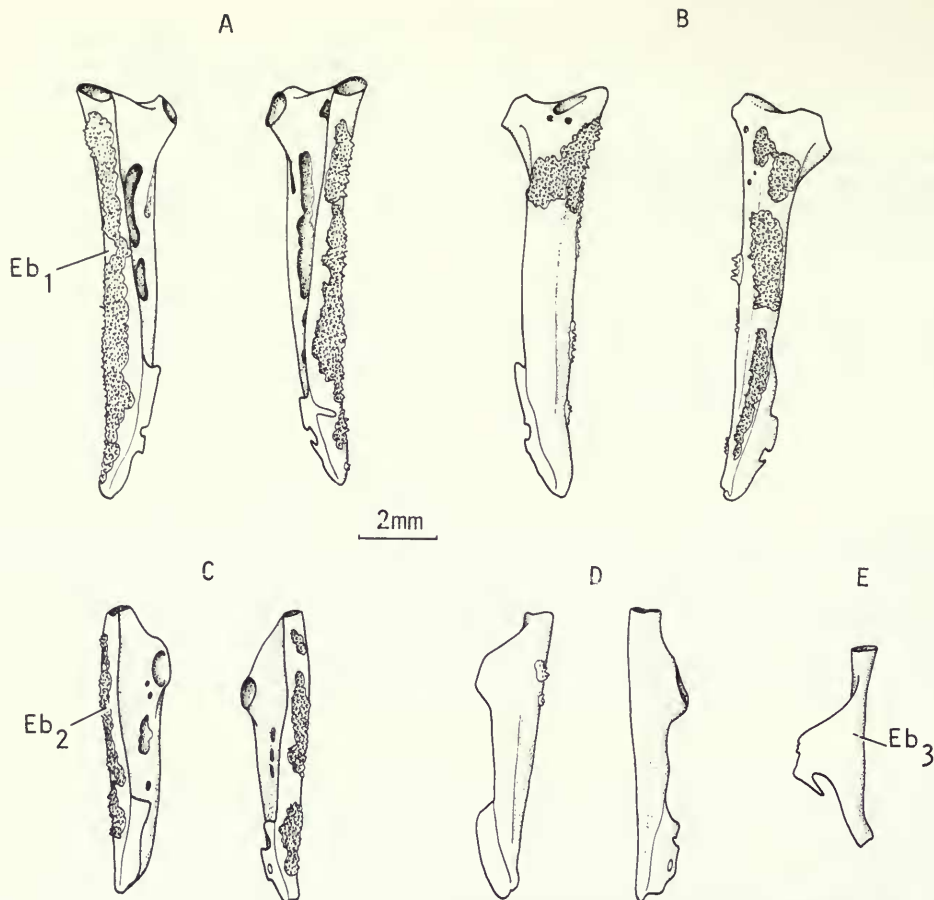


Fig. 116 *Mimia toombsi* Gardiner & Bartram. First epibranchials in (A), dorsal and (B), medial views; second epibranchials in (C), dorsal and (D), medial views; (E), third left epibranchial in lateral view. All from BMNH P.53245.

phlyctaeniids) or *Acanthodes* (Miles 1973a: pl. 4; Jarvik 1977: 207) and this is considered the primitive gnathostome condition.

The hyomandibula in *Mimia*, *Moythomasia* and *Eusthenopteron* bears a single, medial row of toothplates along its anterior margin. Jarvik (1954: 46) has homologized the toothplates of *Eusthenopteron* with the accessory hyomandibula (= dermohyal) of *Polypterus*. But in *Mimia* and *Moythomasia* there are both lateral hyomandibular toothplates and a dermohyal. A medial patch of toothplates has been recorded on the hyomandibula of *Nesides* (Bjerring 1977) and *Latimeria*, and in *Elops* there is a row, much as in *Mimia*. Nybelin (1968: 441) has suggested that this series in *Elops* may be serially homologous to the medial epibranchial toothplates on the gill-arches. In *Elops* the epibranchial toothplates alternate with the gill-rakers, and both Nybelin (1968) and Nelson (1969b, 1970b) have postulated that gill-rakers are modified toothplates. Gill-rakers occur on the hyomandibula of *Acanthodes* where their presence has been taken as indicative of an open hyoid gill-slit (Watson 1937, Nelson 1968). However, Ørvig (1973: 146) and Jarvik (1977: 210) have suggested that these gill-rakers in acanthodians are endoskeletal and are therefore homologous with the cartilaginous rods which support the so-called 'gill-rakers' in sharks and dipnoans. In *Acanthodes* the hyomandibular gill-rakers form a single series which projects ventromedially into the pharynx (Miles 1973a). A similar single series of hyomandibular gill-rakers has been recorded in the selachian *Cetorhinus*, the

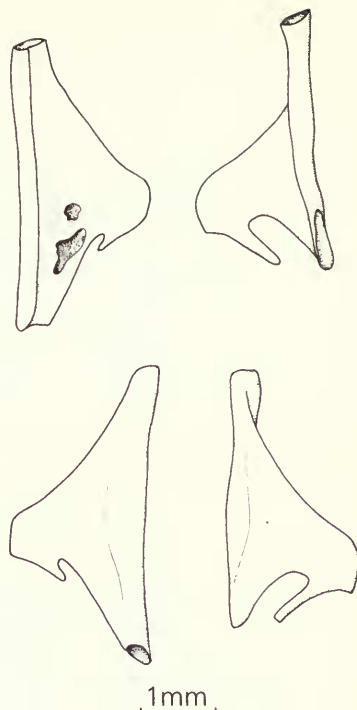


Fig. 117 *Mimia toombsi* Gardiner & Bartram.
Third epibranchials in dorsal (above) and
ventromedial views, from P.56474.

holocephalan *Callorhynchus* and the teleost *Neonesthes* (Holmgren 1942, Miles 1973a). There is therefore no need to invoke the aphetohyoid hypothesis to explain their occurrence in acanthodians. Whether or not hyomandibular gill-rakers are a primitive gnathostome feature is uncertain; from their distribution within the phylogeny they appear to have arisen on more than one occasion.

The remainder of the hyoid arch may consist of one further cartilage (= ceratohyal) as in chondrichthyans, or several as in osteichthyans.

In osteichthyan fishes there is invariably a separate ossification or cartilage linking the hyomandibula with the ceratohyal, the interhyal, and this is considered synapomorphous for the group. In Recent chondrosteans the cartilage is hypertrophied and has often been incorrectly referred to as a symplectic (Gardiner 1973, Patterson 1982). An accessory element between the hyomandibula and the ceratohyal has been described in one specimen of *Acanthodes* (Miles 1973a: fig. 15; pl. 7) but the evidence is equivocal (see BMNH P.4990).

In osteichthyans there is a further separate ossification or cartilage in front of the ceratohyal, the hypohyal. This, like the interhyal, is synapomorphous for that group. In teleosts other than pholidophorids and some osteoglossomorphs the hypohyal contains two ossifications (Patterson 1982).

The single ventral hyoid cartilage (called ceratohyal) of chondrichthyans is matched in acanthodians. In *Acanthodes* (Fig. 120) it is perichondrally ossified in two sections (one at either end), like the hyomandibula, epibranchials and ceratobranchials (Miles 1973a). This has allowed the anterior ossification to be mistaken for a hypohyal (Watson 1937: fig. 18A; Nelson 1968: fig. 3A, B), but in presumed mature individuals of *Acanthodes* the ceratohyal is all one ossification (BMNH P.49977). It is therefore simpler to regard this mode of ossification as synapomorphous for acanthodians.

In many osteichthyans there is either a single ceratohyal ossification (*Cheirolepis*, *Mimia*, *Polypterus*, *Glyptolepis*, *Latimeria*) or a single cartilage (*Neoceratodus*, *Necturus*). In neopterygians (*Pteronisculus*, *Lepisosteus*, *Amia*, teleosts), however, the ceratohyal is ossified

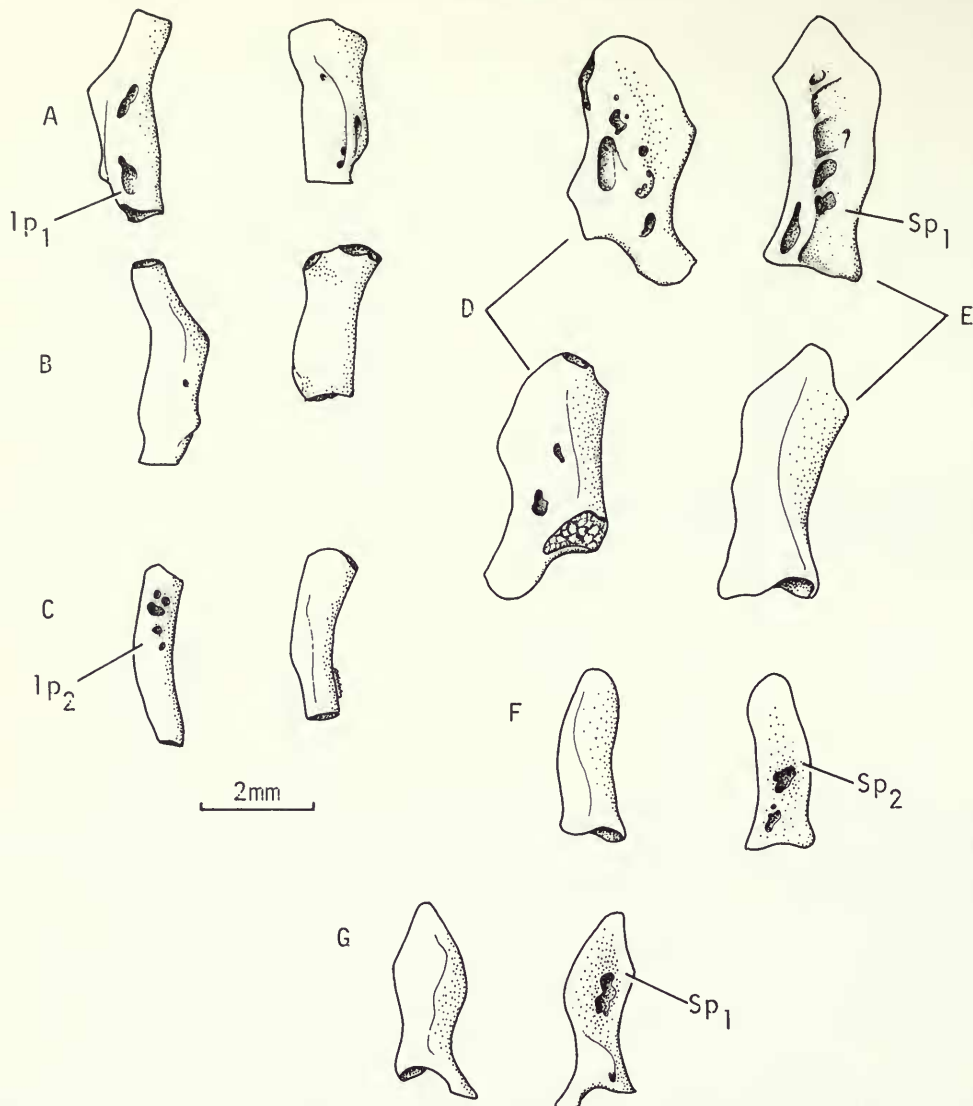


Fig. 118 Infrapharyngobranchials and suprapharyngobranchials. A–C, E, G, *Mimia toombsi* Gardiner & Bartram. (A) first infrapharyngobranchials in dorsal and (B) ventral views; (C) second left infrapharyngobranchial in dorsal view, second right in ventral view; (E) first right suprapharyngobranchial in medial (top) and lateral views; all from P.53245. (G) second left suprapharyngobranchial in lateral (left) and medial views, from BMNH P.56474. D, F, *Moythomasia durgaringa* Gardiner & Bartram. (D) first right suprapharyngobranchial in medial (top) and lateral views; (F) second right suprapharyngobranchial in lateral (left) and medial views; both from BMNH P.53256.

in two sections which parallel those in *Acanthodes*, while in recent chondrosteans there are two separate cartilages (ceratohyal and interhyal of previous authors, but see Patterson 1982). The posterior ceratohyal cartilage in *Polyodon* carries a branchiostegal ray, as does the posterior ceratohyal in *Lepisosteus*. Two ceratohyal cartilages are considered to be a unique feature of chondrosteans and two ceratohyal ossifications a synapomorphy of neopterygians, where they always remain separate and do not fuse as they do in acanthodians.

The remaining element in the hyoid arch is the symplectic. There are three kinds of symplectic

recorded in fishes (Gardiner 1973, Patterson 1973, 1982); that in Recent chondrosteans, which is probably a hypertrophied interhyal, that in neopterygians, which is confluent with the hyomandibula, and that in actinistians. The neopterygian symplectic develops as an anteroventral outgrowth of the hyomandibular cartilage which ossifies independently. It therefore remains intimately attached to the hyomandibula and is applied to the quadrate in teleosts or to the quadrate and lower jaw in halecomorphs (Patterson 1982). This type of symplectic is considered synapomorphous for neopterygians (Patterson 1973: 262).

In *Latimeria* the symplectic is a large, partly ossified, independent cartilage which is connected by a ligament to the hyomandibula. It articulates with the interhyal and ceratohyal dorsally and with the lower jaw ventrally. The articulation with the lower jaw is posterior to and separate from that between the quadrate and lower jaw. These articulations are therefore in tandem (Forey 1981) and not side by side as in halecomorphs. Like Forey (1981), I consider this tandem double jaw articulation synapomorphous for actinistians, and like Patterson (1982) I regard the actinistian symplectic as characteristic of that group and non-homologous with the neopterygian symplectic.

2. Basibranchial and branchial arches

Normally in gnathostome fishes there is a series of five arches (Nelson 1969*b*). Dorsally they consist of paired epi- and pharyngobranchials and ventrally of paired hypo- and ceratobranchials.

There are hypobranchials in the first four arches in many osteichthyans, though in *Acipenser* and most teleosts (Patterson 1977*a*) only the first three are developed. Four hypobranchials are also present in most chondrichthyans, and this is believed to be the condition in acanthodians (Nelson 1968, Miles 1973*a*). However, the structures which Miles (1973*a*) identified as hypobranchials in *Acanthodes* have been alternatively interpreted as basibranchials by Rosen *et al.* (1981), and in turn the hypobranchials of Watson (1937) and Nelson (1968, 1969*b*) have been interpreted as anterior ceratobranchials by Miles (1973*a*). Re-examination of Watson's and Miles' material has persuaded me that the ceratobranchials are perichondrally ossified in two portions and that the ossifications lying anterior to the second, third and fourth are hypobranchials (Miles 1973*a*: fig. 18, hy.br 2-4) and not basibranchials as Rosen *et al.* (1981) presumed. The ossifications in question are inturned anteriorly and a single basibranchial (Fig. 120) against which the ceratohyal and first ceratobranchial articulated can be seen in several specimens (e.g. BMNH P.49977; Miles 1973*a*: pl. 5B, b.br). Often, only the anterior end of the

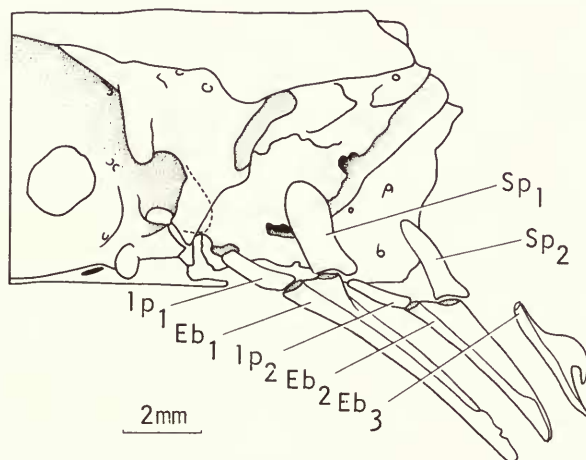


Fig. 119 *Mimia toombsi* Gardiner & Bartram. Reconstruction of posterior part of the neurocranium and dorsal gill-arch elements in lateral view.

basibranchial is ossified (basihyal of Watson 1937, and see BMNH P.49933, P.44934). There is no hypobranchial in the first arch in *Acanthodes*.

The basibranchial in chondrichthyans usually consists of two large, distinctly separated cartilages or copulae, but subdivision of these may occur, particularly in holocephalans. The ceratohyal and first branchial arch often articulate with the anterior cartilage (*Heterodontus*, *Heptanchus*, *Squatina*) and the first arch slants obliquely forwards and downwards. The succeeding hypobranchials point backwards to meet the anterior border of the posterior cartilage, and this is considered synapomorphous for chondrichthyans.

In actinopterygians a single basibranchial ossification has been reported in *Polypterus*, *Mimia* and *Moythomasia*. In the Gogo palaeoniscids the basibranchial is composed of three ossification centres which presumably fused during ontogeny, and which were obviously in the same cartilage. They correspond to the three basibranchials of *Pteronisculus* and *Birgeria* and to the three minute ossifications recorded in the cartilaginous basibranchial of *Acipenser* by van Wijhe (1882). In *Polyodon* and teleosts there are three separate cartilages, but in *Lepisosteus* and *Amia* there are four. The first three copulae in *Lepisosteus* and the second in *Amia* are perichondrally ossified. The segmentation seen in the basibranchials of *Amia* and *Lepisosteus* must have occurred independently in each form and four copulae cannot be regarded as synapomorphous for neopterygians (cf. Wiley 1976). The basibranchial in *Polypterus* comprises a single ossification which possibly corresponds to the first or anterior ossification in *Mimia* and *Pteronisculus* (Patterson 1982).

Elsewhere in osteichthyans a basibranchial consisting of more than one ossification has been described only in *Eusthenopteron* (Jarvik 1954). The division between the two ossifications is in exactly the same position as that between the two anterior ossifications of *Mimia*. Whether these two ossifications are in a single cartilage, as in *Acipenser* and *Mimia*, or represent separate cartilages, as in *Polyodon*, we have no means of knowing.

In *Latimeria*, *Glyptolepis* and *Laccognathus* the copula resembles a greatly foreshortened *Polypterus* basibranchial. The basibranchial of *Neoceratodus* and larval urodeles is similar though considerably reduced. A small, triangular basibranchial has also been described in the Devonian dipnoans *Griphognathus* and *Chirodipterus*. However, Miles (1977) has suggested that the basihyal in these fossils is in fact a co-ossified anterior basibranchial and basihyal and accordingly restored the bases of the first two arches on this ossification. Rosen *et al.* (1981) suggest that if all the arches were restored entirely on the triangular basibranchial then the arrangement of the gill-arch bases would be similar to *Neoceratodus*. Since cartilages rarely fuse during development (although they may divide), and a separate cartilaginous basihyal is present in *Neoceratodus*, I abide by our solution (Rosen *et al.* 1981) and thus a single broad, triangular basibranchial is a synapomorphy of porolepiforms, actinistians and dipnoans (non-homologous with that of *Polypterus*). Other gill-arch synapomorphies of that group include the reduction or loss of hypobranchials in actinistians, dipnoans and larval urodeles and the articulation of the last gill-arch with the base of the preceding arch in porolepiforms, actinistians, dipnoans and larval urodeles (Rosen *et al.* 1981). I further conclude that the primitive osteichthyan possessed a single, cartilaginous basibranchial with at least two ossification centres. A similar basibranchial may have been present in acanthodians (see Fig. 120). In acanthodians and chondrichthyans the hyoid and first gill-arch articulate with the anterior basibranchial and in osteichthyans at least the second gill-arch also articulates with it. This latter condition is synapomorphous for osteichthyans (Rosen *et al.* 1981).

Anterior to the basibranchial a further ossification occurs in advanced actinopterans, *Eusthenopteron* and dipnoans. It is usually referred to as the basihyal (Nelson 1969*b*), though Jarvik (1954) regarded it as a member of the sub-branchial series and accordingly referred to it as the 'sublingual rod'. A cartilaginous basihyal is also found in larval apodans, lizards and *Sphenodon* (de Beer 1937). This should not be confused with the paired processus lingualis of chelonians and birds (also called paraglossum or entoglossum), which appears to be homologous with the anterior horns (or hyoid arch or lesser cornu) of *Echidna* (Goodrich 1930: fig. 474). The basihyal in actinopterans is confined to teleosts where it occurs in

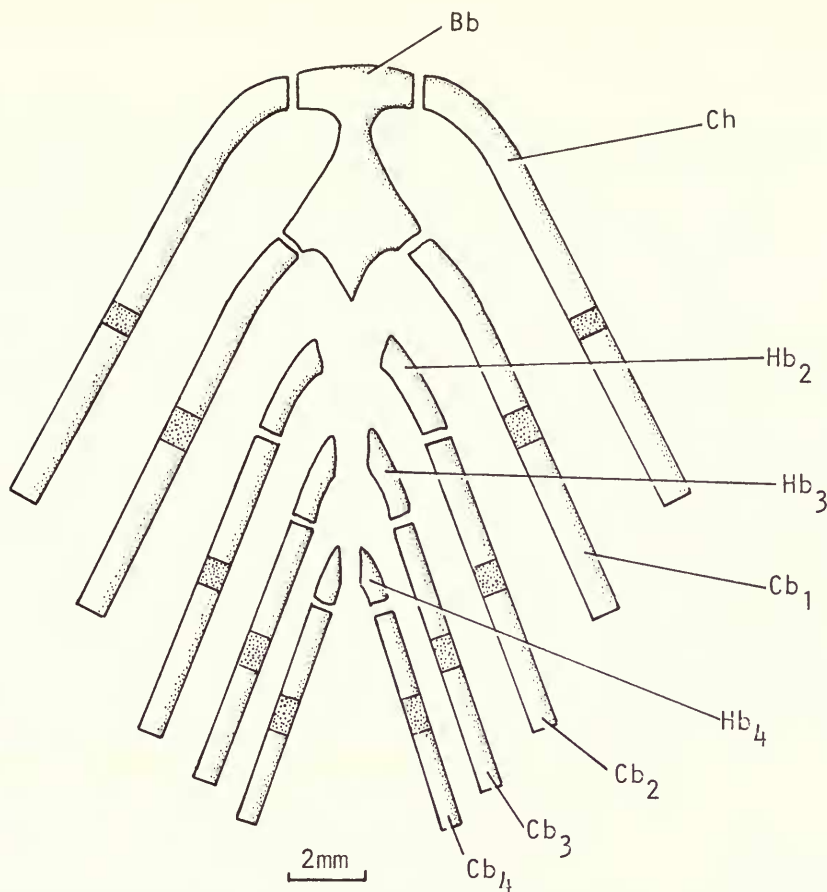


Fig. 120 *Acanthodes bronni* Agassiz. Reconstruction of ventral part of gill-arch skeleton in dorsal view. Based on BMNH specimens.

osteoglossomorphs and those cladistically more derived groups (Patterson 1977a). It appears to chondrify separately from the basibranchial in *Salmo* (de Beer 1937) and *Gasterosteus* (Swinerton 1902), and usually supports a median dermal toothplate which may bear large teeth. The basihyal of *Eusthenopteron* is a long, narrow bone with a strong median ridge dorsally (Jarvik 1954). A similarly-enlarged basihyal is present in *Griffithichthys* where it supports two pairs of toothplates. In *Conchopoma* there is a single, median toothplate. Miles (1977: 286) has suggested that the elongation of the basihyal in *Griffithichthys* may be correlated with secondary elongation of the lower jaw (the basihyal cartilage in *Neoceratodus* remains small) and that the similar basihyals in *Eusthenopteron* and *Griffithichthys* are the result of parallel evolution. The absence of basihyals in actinistians, porolepiforms and primitive actinopterygians and the lack of other plausible synapomorphies between *Eusthenopteron* and dipnoans (Rosen *et al.* 1981) suggest that the basihyal has arisen on at least three occasions (teleosts, *Eusthenopteron*, dipnoans and tetrapods).

Associated with the dorsal surface of the basibranchial is a series of toothplates. Nelson (1969b) hypothesized that the plesiomorphous gill-arch dentition of osteichthyans consisted of six rows of dermal elements, and that paired basibranchial toothplates were primitive for osteichthyans. Paired basibranchial toothplates are found in fossil actinistians where they are arranged in three pairs lying opposite the first three gill-arches (Forey 1981). In *Latimeria* the

toothplates are insignificant and according to Nelson (1969b) are an adventitious formation. If Forey's (1981) phylogeny of the actinistians is correct this would seem to be the most parsimonious hypothesis. In *Eusthenopteron* (Jarvik 1954) there are two pairs of toothplates on each basibranchial, and also a lateral row of smaller plates related to the hypobranchials. In *Mimia* and *Moythomasia* there are numerous, irregularly-arranged small toothplates over the whole dorsal surface of the basibranchials and in *Polypterus* two widely-separated rows of asymmetrical plates which come together posteriorly. In *Acipenser* (Jollie 1980) two transverse bands of teeth cross the copula at the level of hypobranchials 1 and 2. In *Bobasatrania*, *Errollichthys* and in teleosts other than Pachycormiformes a median toothplate covers the basibranchials. These observations suggest that primitively the osteichthyan basibranchial was covered by numerous toothplates which have been aligned into four rows in *Eusthenopteron*, and into two rows in actinistians (and *Griphognathus*). There is a median plate in teleosts (and *Conchopoma*).

Situated beneath the basibranchial and joined anteriorly by ligaments to the hypohyals is a median bone, the urohyal (in *Polypterus* the ligaments are ossified). In actinopterygians a urohyal occurs in *Polypterus*, *Australosomus* (Patterson 1977b) and teleosts. In *Australosomus* and pholidophorids it is presumed to ossify in cartilage bone, but in *Polypterus* and extant teleosts it ossifies in membrane bone. Patterson (1977b) has convincingly demonstrated the dual nature of the teleostean urohyal and has hypothesized that it represents the fused interclavicle and urohyal, the interclavicle having sunk beneath the surface. Interestingly the interclavicle has also sunk beneath the surface in many actinistians (Forey 1981). An endochondral urohyal also occurs in Devonian and Carboniferous actinistians, *Latimeria*, porolepiforms, osteolepiforms (Jarvik 1963), Devonian dipnoans (Miles 1977), urodeles and anurans (Jarvik 1963, Patterson 1977b). The urohyal is presumed to have remained cartilaginous in the Gogo palaeoniscids and *Pteronisculus*. The presence of a urohyal is therefore hypothesized as plesiomorphous for osteichthyans.

Turning to the dorsal parts of the arches we find that in some actinopterygians and sarcopterygians there are two types of pharyngobranchials, infra- and suprapharyngobranchials. The presence of the latter has been regarded as a synapomorphy of osteichthyans by Rosen *et al.* (1981).

Allis (1925) and Holmgren (1942) suggested, mainly on evidence of orientation, that the osteichthyan suprapharyngobranchial was homologous with the chondrichthyan pharyngobranchial. By contrast Nelson (1968) homologized the infrapharyngobranchial with the chondrichthyan (and acanthodian) pharyngobranchial because in both groups they support the pharyngeal roof and denticles. Nelson (1968) also suggested that the condition in the first arch of *Eusthenopteron*, where there is a presumed compound supra-infrapharyngobranchial, could be primitive for osteichthyans and might be the equivalent of the pharyngobranchial of *Acanthodes*. He further imagined that the dorsal process of an *Acanthodes* pharyngobranchial might be the homologue of the suprapharyngobranchial. Miles' (1973a: fig. 16) redescription of the pharyngobranchials of *Acanthodes* has firmly persuaded me of the efficacy of Nelson's (1968) hypothesis that the form of the pharyngobranchials of *Acanthodes* is primitive for gnathostomes. Thus I believe that the acanthodian pharyngobranchial is homologous with that of chondrichthyans and both the infra- and suprapharyngobranchials of the anterior arches of osteichthyans and with the pharyngobranchial of the third arch in actinopterygians.

In *Latimeria*, where the first pharyngobranchial is a single, slender, dorsally-directed rod, both Millot & Anthony (1958) and Nelson (1968) have interpreted it in the light of *Eusthenopteron* and considered it to represent a compound supra-infrapharyngobranchial. But this rod appears serially homologous with the second suprapharyngobranchial, and furthermore the contact between the first infrapharyngobranchial and the braincase seen in primitive actinopterygians and *Eusthenopteron* is replaced in *Rhabdoderma* by a direct contact between the first epibranchial and the braincase (Forey 1981). Both the first and second epibranchials contact the braincase in *Latimeria*. An analogous articulation occurs between the first epibranchial and the auditory capsule in *Polypterus*, but here the infrapharyngobranchial remains and articulates in the angle of the parasphenoid, as in *Amia* and some teleosts. In most

teleosts the infrapharyngobranchial articulates with the parasphenoid rather than with the prootic (Patterson & Rosen 1977: 129).

Suprapharyngobranchials occur in several actinopterygians, including *Mimia*, *Moythomasia*, *Polyodon*, *Acipenser*, *Pteronisculus*, *Australosomus*, *Lepisosteus* and teleostean fishes of the families Elopidae and Alepocephalidae (Nelson 1969b); in actinistians (*Latimeria*) and in *Eusthenopteron*. Usually they are two in number. Their absence from the first arch in *Polypterus* is considered derived and related to the contact between the first epibranchial and auditory capsule. Infrapharyngobranchials occur on the first three arches in many actinopterygians, including *Pteronisculus*, *Australosomus*, *Acipenser*, *Lepisosteus* and *Amia*, though it is possible to regard this third infrapharyngobranchial as an undifferentiated pharyngobranchial. There are only two infrapharyngobranchials in *Eusthenopteron* and *Mimia* and one in *Latimeria* (2nd) and *Polypterus* (1st). In Recent teleosts there are four pharyngobranchials.

From this survey I hypothesize that the primitive osteichthyan possess two suprapharyngobranchials (on the first two arches) and that three, not four, pharyngobranchials is plesiomorphic for osteichthyans (cf. Nelson 1969b). Furthermore, the loss of pharyngobranchials (including infra- and supra-) is a synapomorphy of choanates (Rosen *et al.* 1981).

There are usually four pharyngobranchials in chondrichthyans and four have also been inferred in acanthodians (Nelson 1968, 1969b). However, careful examination of the numerous casts of *Acanthodes* made by Dr Roger Miles of material from the Humboldt University, Berlin, the Palaeontological Institute of the University of Bonn and the University Museum of Zoology, Cambridge, failed to reveal more than three pharyngobranchials. Despite some controversy (Miles 1964, 1965, Nelson 1968, 1969b) it is now generally agreed that the pharyngobranchials of *Acanthodes* projected posteromedially into the roof of the pharynx (Miles 1973a). Thus the posterior position of the gill-arches and the posterior orientation of the pharyngobranchials in chondrichthyans and acanthodians are considered to be shared primitive characters.

Axial skeleton

Mimia toombsi

The axial skeleton is represented by dorsal and ventral arcual elements throughout its length and by supraneurals and ribs in the abdominal region. The individual ossifications are perichondral shells. The notochord was persistent and there is no trace of centra.

The dorsal arcual ossifications are always paired and are presumed to be basidorsals. No separate interdorsals have been observed and in this respect *Mimia* resembles *Polypterus*, *Lepisosteus*, teleosts etc. (Gardiner 1983). In the abdominal region each basidorsal ossification (na, Figs 121, 123) consists of a proximal plate or neural arch and a long distal process or neural spine. On the lateral face of the neural arch there is a well-developed, laterally-directed epineural process (epi, Fig. 121). Similar processes in the diapophysial position are found on the anterior vertebrae of *Australosomus*, *Boreosomus* (Nielsen 1949: figs 41, 42, 47, 48), *Caturus* (Gardiner 1960: fig. 33, Patterson 1973: 237) pholidophorids, *Elops* etc. and the dipnoan *Griphognathus* (Rosen *et al.* 1981: fig. 54A). These epineural processes are found on each of the first 14 vertebrae in *Mimia*. That on the first is very stout and terminates in several finger-like projections (Fig. 121D). The bases of all the epineural processes are perforated or notched for the passage of the intersegmental artery. The second basidorsal of *Boreosomus* (Nielsen 1949: fig. 48) likewise has a foramen in its epineural process. The medial faces of the neural arches are devoid of perichondral lining where they embraced the spinal cord. Posterior to the dorsal fin the neural spines decrease in length caudally and towards the end of the tail some of the basidorsals are incompletely segmented from one another and the junction between them is marked by foramina for the spinal nerves. This is particularly marked in *Moythomasia* (BMNH P.53255).

Above the basidorsals of the abdominal region there is a series of unpaired supraneurals. This series terminates a short distance in front of the dorsal fin (Fig. 124).

The ventral arcual elements are unpaired and are presumed to represent basiventrals. In the abdominal region these elements are semicircular in cross section with a posteriorly-directed

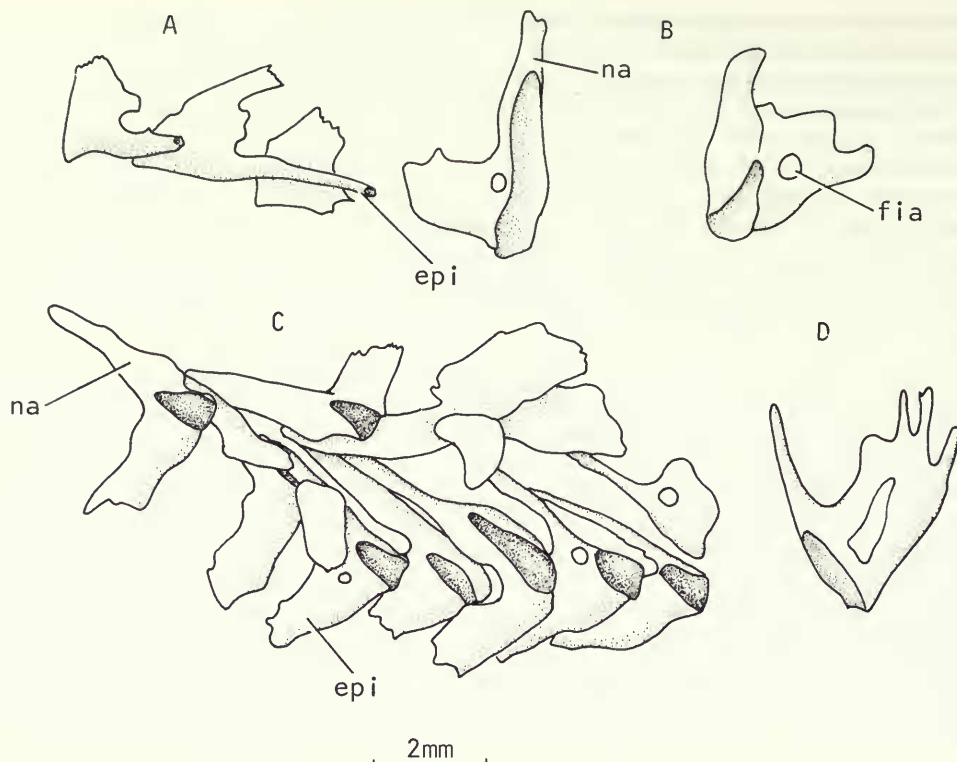


Fig. 121 *Mimia toombsi* Gardiner & Bartram. Neural arches and spines from anterior part of vertebral column in (A) lateral and (B), (C), (D) anteromedial views. (A) from Western Australian Museum no. 70.4.245 (holotype), (B) from BMNH P.56500, (C) and (D) from BMNH P.53228.

median keel similar to that in *Pteronisculus* (Nielsen 1942: fig. 49). Ossified ribs articulated with the lateral face of the abdominal basiventrals. In the region of the anal fin the ventral arcual elements or haemal arches have well-developed median haemal spines (ha, Fig. 122A, B, C, D, E, G) whose bases enclose the aortic or haemal canal. The lateral faces of the haemal arches in this region are perforated by foramina for the intersegmental arteries (fia, Fig. 122C), as in *Caturus* (Rosen *et al.* 1981: fig. 59A, B). Occasionally the roof of the haemal canal may also have a median perforation (Fig. 122E).

In the caudal region there is a series of 22 stout hypurals which decrease in length posteriorly (Fig. 124). The caudal lepidotrichia embrace the ends of these hypurals.

Moythomasia durgaringa

In several specimens remnants of the axial skeleton are visible and these appear to be identical with those of *Mimia*. However, in the caudal region the neural arches and their spines are fused and the neural spine is median, as in the caudal region of *Birgeria*.

Axial skeleton: discussion

1. Arcualia

Four pairs of arcualia were primitively present in each segment of gnathostomes (Gardiner 1983), and in all osteichthyans they are represented by ossified or cartilaginous elements in at least part of the vertebral column. In actinopterygians they occur throughout the whole column in *Acipenser* and *Polyodon*, in *Pteronisculus* they are restricted to the abdominal region and in *Australosomus*, *Caturus* and *Pholidophorus* to the caudal region. Separate interdorsals and

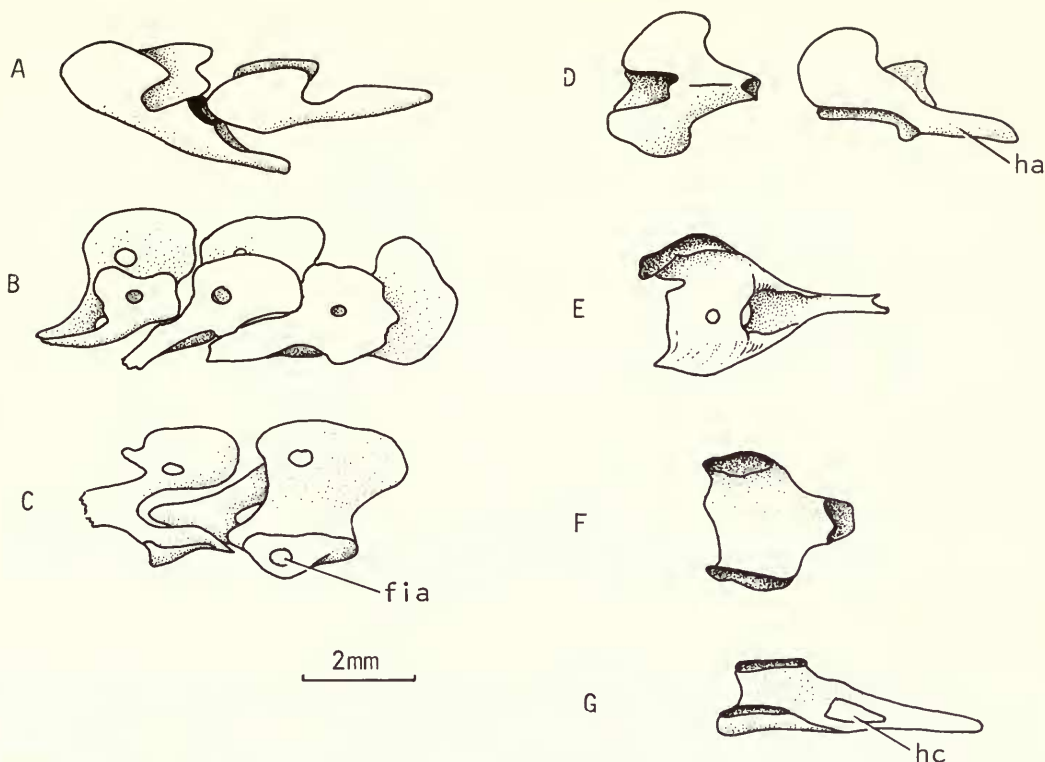


Fig. 122 *Mimia toombsi* Gardiner & Bartram. Haemal arches from the anterior part of the caudal region in (A), (B) lateral, (C), (G) dorsolateral, (E), (F) dorsal, and (D) ventral views. (A), (B), (C) from Western Australian Museum no. 70.2.245 (holotype), (D) from BMNH P.53232, (E) from BMNH P.56494, (F) and (G) from BMNH P.56500.

interventrals are missing in *Polypterus* and *Lepisosteus*, and from the development of most teleosts; separate intervertebrals are missing from the trunk of developing *Amia*.

In actinistians (*Latimeria*) the full complement of arcualia is confined to the caudal region; in *Neoceratodus* the two dorsal pairs are present only in the caudal area whereas the two ventral pairs are only found in the anterior trunk. In *Eusthenopteron*, *Osteolepis*, *Glyptolepis* and most temnospondyls the two dorsal pairs are always present although ventrally there is only a single element. However, as in *Latimeria*, the full complement is seen in the tail region of several tetrapods (*Archegosaurus*, *Chelydosaurus*).

2. Centra

The earliest recorded actinopterygian centra are the thin, ring centra of *Haplolepis* (Baum & Lund 1974) from the Upper Carboniferous. These ring centra comprise thin calcifications in the notochordal sheath and are developed from dorsal and ventral hemicentra. Similar ring centra occur in the tail of *Pygopterus*, but in *Turseodus* there are separate dorsal and ventral hemicentra.

Chordacentra appear to have been independently acquired in the pholidopleurids, and in *Australosomus* (Nielsen 1949) they are overlain by endochondrally ossified neural and haemal arches and interdorsals. By the end of the Jurassic many actinopterygians possessed calcifications in the notochordal sheath including hemichordacentra in *Furo philpotae* (Agassiz) and *Caturus* and complete chordacentra in pholidophorids, archaeomaenids, some pachycormids, pleuropholidids, catervariolids, *Galkinia* and *Ichthyokentema* (Patterson 1973). Today the notochordal sheath is still involved in the early ontogenetic stages of centrum formation in

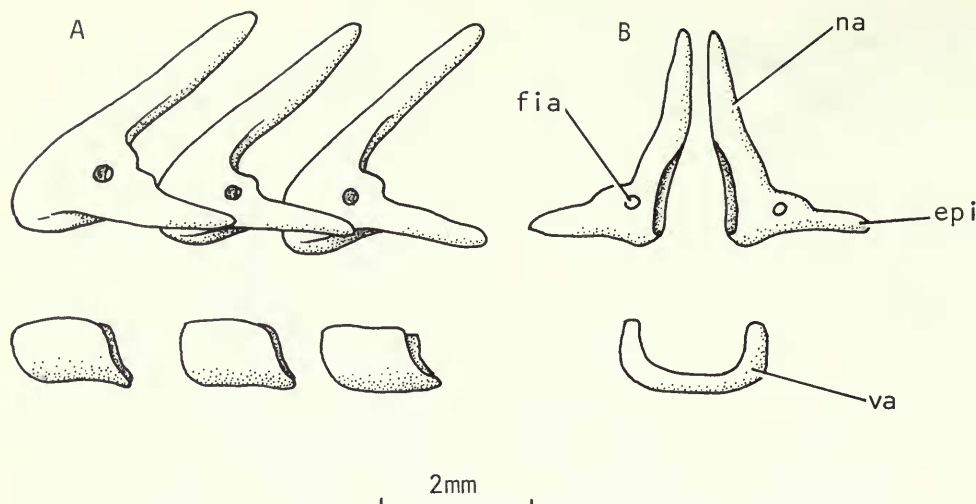


Fig. 123 *Mimia toombsi* Gardiner & Bartram. Restoration of part of the vertebral column from the anterior abdominal region: (a), lateral view, (b), anterior view.

primitive living teleosts and if our phylogenies are correct (Patterson 1973, 1977a, Rosen *et al.* 1981) then chordacentra must have arisen on at least three occasions within the actinopterygians (haplolepidids, pholidopleurids and halecostomes).

By the Cretaceous several groups of actinopterygians had acquired much more substantial centra in the form of perichordal cylinders of membrane bone. Such groups include caturids (*Neorhombolepis*, *Macrepistius*), macrosemiids (*Macrosemius*, *Ophiopsis*), aspidorhynchids (*Belonostomus*) and oligopleurids (*Ionoscopus*, *Callopterus*). Perichordal, membrane bone centra are also developed in *Polypterus*, *Lepisosteus*, *Amia* and Recent teleosts (Gardiner 1983). From this we may conclude that membrane bone centra have developed at least five times within the actinopterygians (*Polypterus*, *Lepisosteus*, *Amia*, aspidorhynchids and teleosts) and possibly as many as seven (oligopleurids and macrosemiids).

Simple, ring-shaped centra resembling those of *Amia* are found in several rhipidistians including *Rhizodopsis*, *Megalichthys*, *Ectosteorhachis* and *Strepsodus*. But the earliest ossified centra belong to the Devonian dipnoans *Griphognathus*, *Rhynchodipterus*, *Soederberghia* and *Chirodipterus*, where they are spool-shaped and presumed to be made up of cartilage bone, as in amniotes.

3. Ribs

In some actinopterygians there is a single series of ribs in the wall of the coelom. These are the ventral or pleural ribs and they develop centrifugally from cartilaginous anlagen close to the vertebra. In cladistians and teleosts there are in addition dorsal ribs in the horizontal septum. These develop from cartilaginous anlagen beneath the lateral line, at the outer junction of the horizontal and transverse septa. Many teleosts have yet a further series of ribs, the so-called epineurals in the epaxial musculature.

The dorsal ribs in *Polypterus* are confined to the middle part of the trunk where they are borne on hypertrophied parapophyses. They are peculiar in that they are firmly tied distally to the lateral line scales (Pearson 1981). The dorsal (epipleural) ribs of teleosts, on the other hand, are usually attached by ligaments to the centrum or in the posterior region to the ventral ribs themselves. They are believed to have arisen within the teleosts and to characterize elopoccephalans and certain osteoglossomorphs (Rosen *et al.* 1981). Dorsal ribs are a primitive attribute of neither actinopterygians nor osteichthyans. Thus it follows that the ribs of

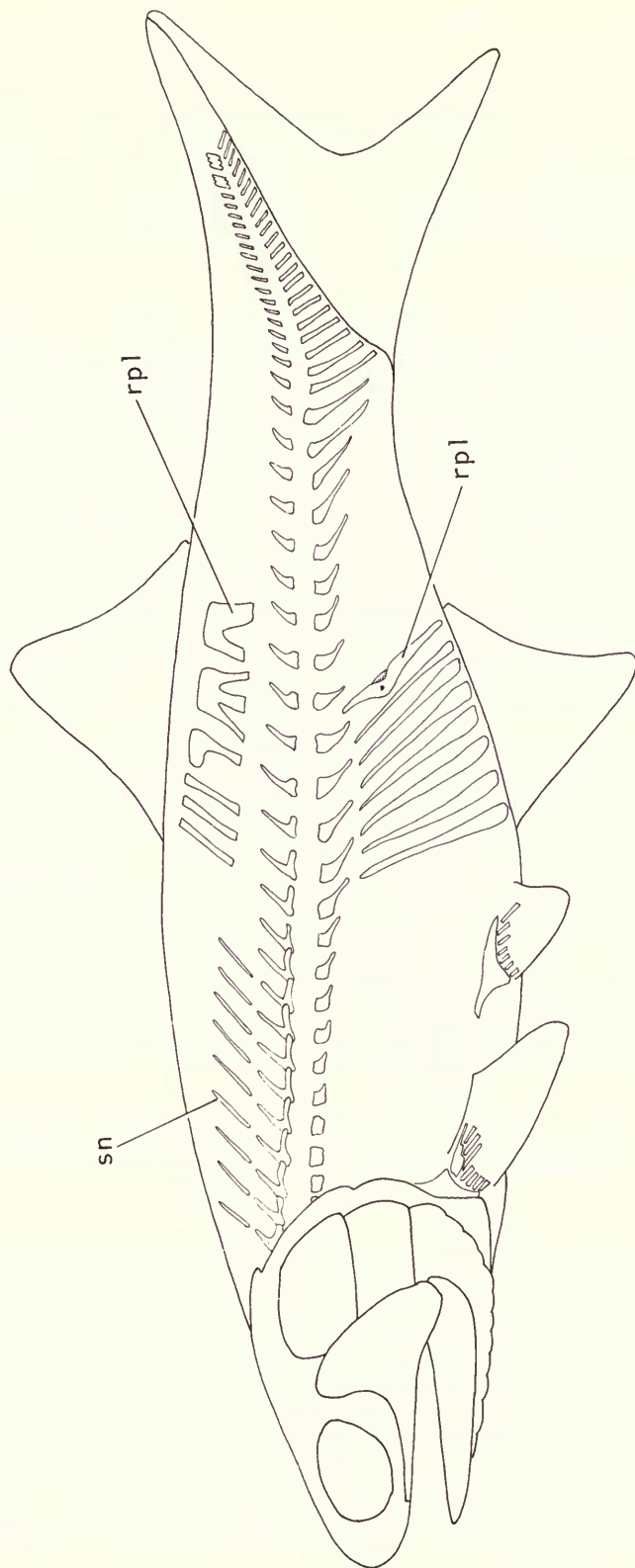


Fig. 124 *Mimia toombsi* Gardiner & Bartram. Attempted restoration of the axial skeleton and endoskeleton of the fins.

chondrichthyans and osteichthyans (other than cladistians and teleosts) are homologous and of the pleural (ventral) type.

Although separate epineural intermuscular (epineural) ribs are synapomorphous for teleosts the primitive condition seems to be an outgrowth or process of the neural arch (Patterson 1973: 237; Rosen *et al.* 1981: 244). They are in the diapophysial position; that is, they are where the bicapital rib of a tetrapod articulates with the base of the neural arch. As Rosen *et al.* (1981) have pointed out, these diapophysial outgrowths in actinopterygians and dipnoans show a morphogenetic gradient which decreases with distance from the occiput; the ribs of primitive tetrapods show a similar gradient.

4. Supraneurals and neural spines

Supraneurals are median, cartilaginous or bony structures that lie above the neural spine and the dorsal ligament. They are often confused with median neural spines which may also project above the dorsal ligament but which are formed by the fusion of the right and left halves of the neural arch. The supraneurals may rest on the dorsal ligament (*Lepisosteus*) or articulate with the neural spines (*Acipenser*, *Protopterus*), or sit on or between the tips of the neural spines (*Leptolepis*, chondrichthyans such as *Notorhynchus*). Primitively they form an extensive series and in *Pteroniscus*, *Phanerotheon*, *Hypsocormus* and *Leptolepis* they extend from occiput to dorsal fin. In the porolepid *Glyptolepis* (Andrews & Westoll 1970) they are even more extensive. In many actinopterygians they are confined to the anterior few segments (*Amia*, *Salmo*) and in others they are missing altogether (*Polypterus*, many teleosts).

Supraneurals are also found in many Recent chondrichthyans, where they are usually confined to the anterior few segments and to the caudal region (= epurals). Occasionally they extend back as far as the anterior dorsal fin and beyond (*Rhina*). Supraneurals are absent in acanthodians.

The neural spines are paired in primitive actinopterygians and median neural spines are considered to be a halecostome characteristic (Patterson 1973: 296). Median neural spines, however, also occur in the caudal region of *Moythomasia*, *Australosomus*, *Birgeria* (Nielsen 1949) and *Haplolepis* (Baum & Lund 1974: fig. 1a), as well as of *Polypterus* where they are formed from membrane bone (Gardiner 1983).

Paired neural spines are found in *Acanthodes*, ptactodonts (personal observation) and many chondrichthyans (*Mustelus*, *Rhina*, *Chimaera*), and this is considered to be the primitive gnathostome condition. In other Recent chondrichthyans the neural arches join below the dorsal ligament (*Lamna*, *Cetorhinus*, *Squalus*), but in halecostomes, *Eusthenopteron*, *Griphognathus* and tetrapods they join above it. Median neural spines are also found in the placoderm *Jagorina* (Stensiö 1959: figs 61, 63), the rhipidistians *Thursius*, *Megalichthys* and *Osteolepis* (caudal region only, Andrews & Westoll 1970: figs 6, 7c, d), *Latimeria*, dipnoans and tetrapods.

Shoulder girdle and pectoral fin

Mimia toombsi

The girdle consists of four paired dermal bones arranged in an overlapping series, post-temporal, supracleithrum, cleithrum and clavicle, with a median interclavicle ventrally. The endoskeletal shoulder girdle is attached to the ventromedial surface of the cleithrum.

The post-temporal (Fig. 125) is a four-sided rectilinear bone which overlaps the supracleithrum posteroventrally. The bone is slightly curved and its anterolateral margin has an unornamented ledge where it is overlapped by the extrascapular. The main lateral line passes through the centre of radiation which lies near the anteroventral corner of the post-temporal.

The supracleithrum is a long, narrow bone which tapers ventrally where it fits over the dorsal tip of the cleithrum. Its centre of radiation lies near the anterodorsal corner and like the post-temporal is pierced by the main lateral line which passes through the bone two-thirds of the way down its posterior margin.

The cleithrum is a large, high bone with a strongly concave anterior margin which forms the

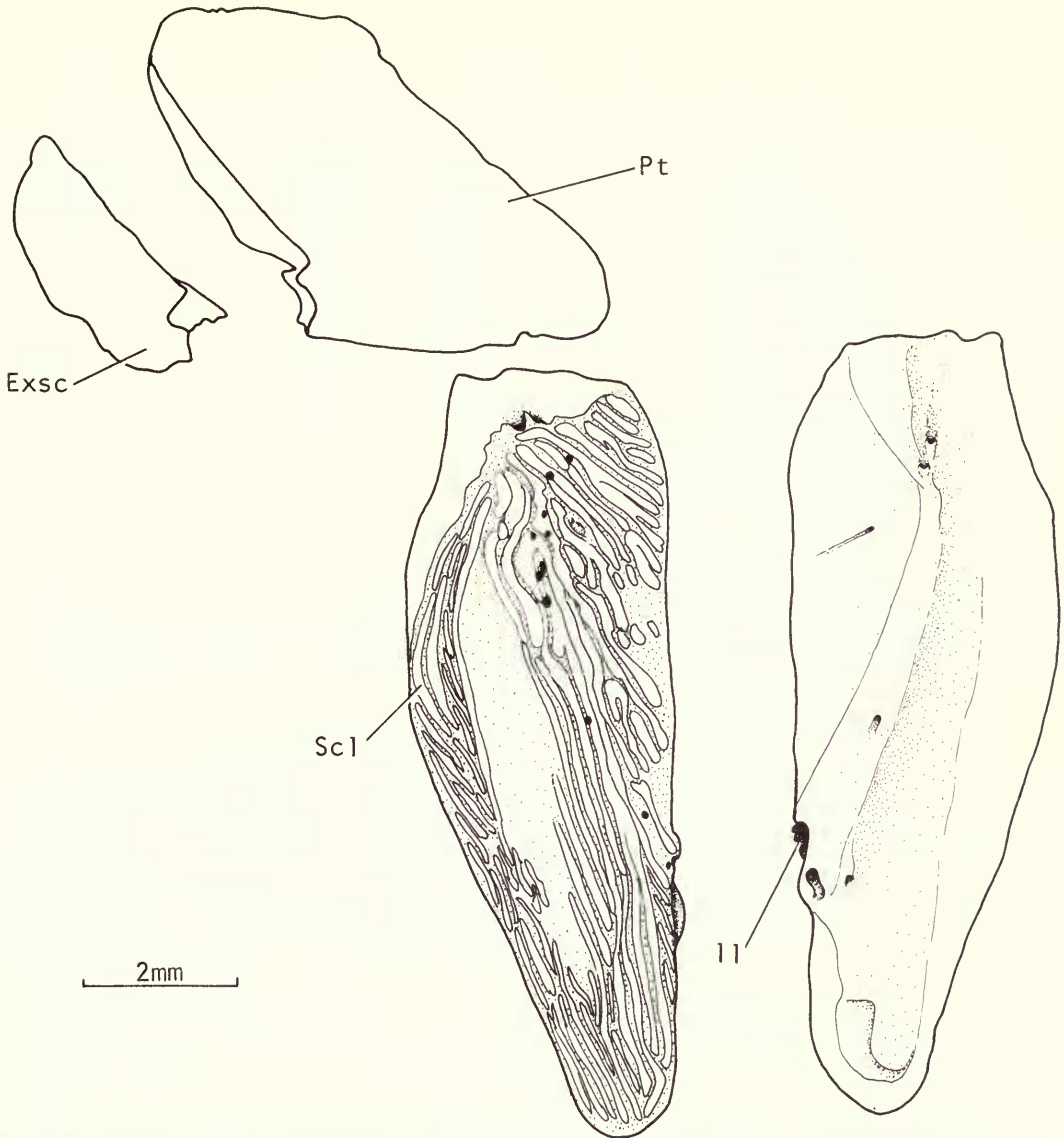


Fig. 125 *Mimia toombsi* Gardiner & Bartram. Left supracleithrum in lateral (left, with outline of post-temporal and extrascapular) and medial views. From BMNH P.56498.

posterior boundary to the branchial cavity. Posteriorly the strongly convex margin is deeply notched ventrally at the point of insertion of the pectoral fin. Ventrally the cleithrum is curved in a medial direction where it is overlapped by the clavicle. The centre of ossification lies anterior and slightly dorsal to the notch for the pectoral fin. The cleithrum is ornamented with stout ridges of ganoine apart from the overlapped areas and the inner edge of the dorsal division.

The clavicle is also a large bone (Figs 126, 130) which curves strongly inwards ventrally, almost to meet its fellow of the opposite side. The clavicle consists essentially of two parts, a large, flat, ventral expanse and a dorsal vertical portion which wraps round the cleithrum. In lateral view the dorsal division is triangular in outline with a long dorsal process. The clavicle is ornamented in the same way as the cleithrum, with long ridges of ganoine. The centre of radiation lies at the junction between the dorsal and ventral divisions. There is no evidence of

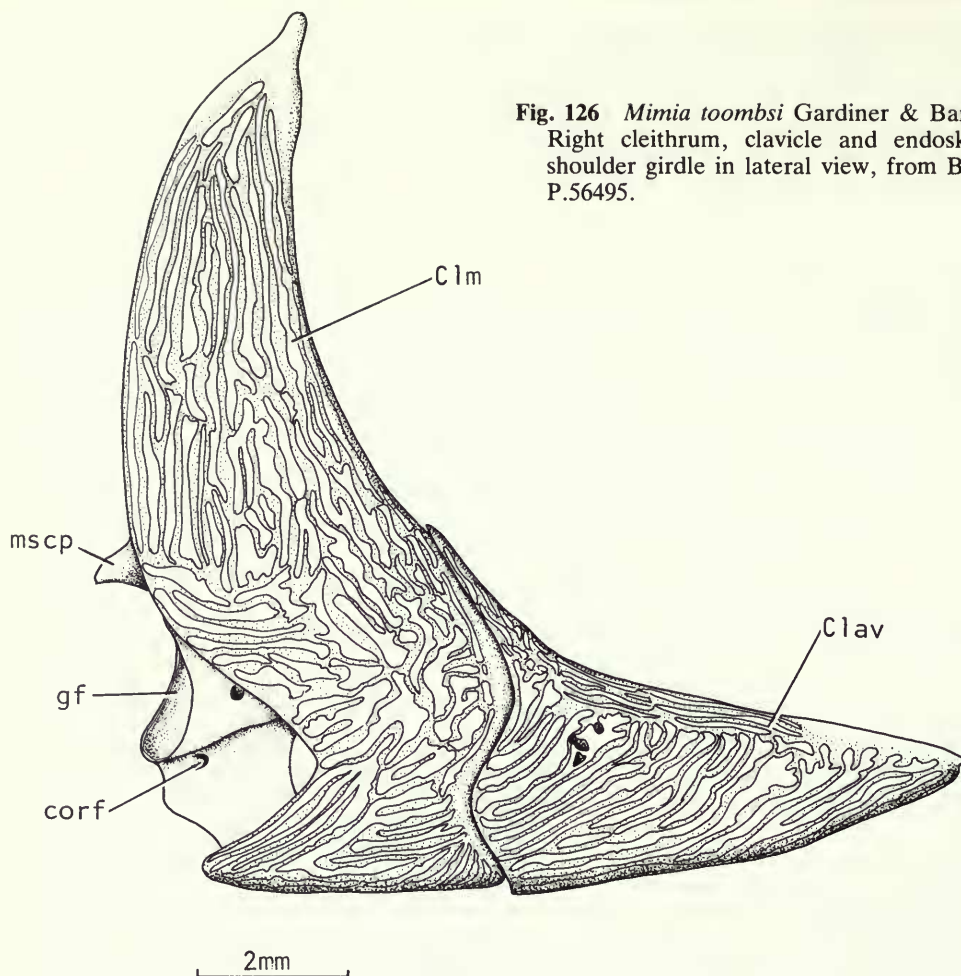


Fig. 126 *Mimia toombsi* Gardiner & Bartram. Right cleithrum, clavicle and endoskeletal shoulder girdle in lateral view, from BMNH P.56495.

the medial process seen in *Acipenser* (Jessen 1972: pl. 15) and said to be present in *Acrorhabdus* (Stensiö 1921: 229).

The interclavicle lies between the clavicles. It is a small ovoid ossification with a few blobs of ganoine along its mid-line.

In cladistians and chondrosteans the two clavicles meet in the mid-line and exclude the interclavicle from the ventral surface (*Acipenser*, *Scaphirhynchus* Jollie 1980, *Polypterus* Fuchs 1929). This is considered a derived character because an interclavicle similar to that of *Mimia* separates the cleithra in osteolepiforms, porolepiforms, primitive actinistians and tetrapods.

Behind the girdle there is a small postcleithrum (Fig. 127). This bone is little more than a magnified flank scale with a much enlarged peg and a ventral projection. The peg is overlapped by the supracleithrum (Rosen *et al.* 1981: fig. 39B). In *Pteronisculus* the connection with the cleithrum is less intimate and the postcleithrum may only be distinguished from the surrounding flank scales by its slightly larger size. In *Acipenser* (Jollie 1980) the postcleithrum lies largely behind the margin of the supracleithrum and in *Lepisosteus* it is the most dorsal member of a row of modified scales.

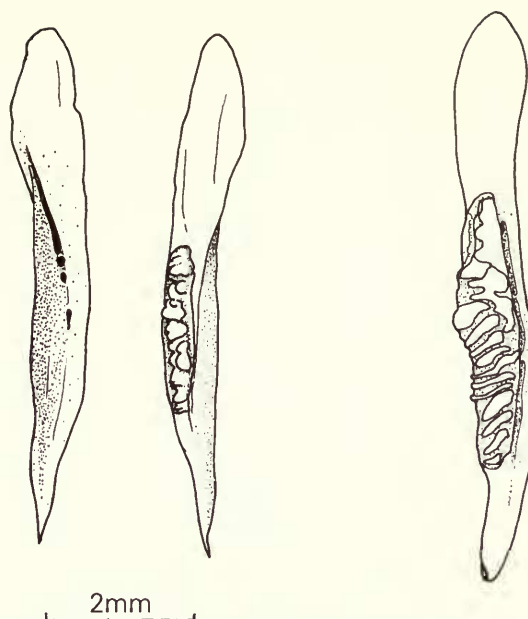


Fig. 127 *Mimia toombsi* Gardiner & Bartram. Postcleithra. (A), right postcleithrum in medial (left) and lateral views, from BMNH P.56484. (B), right postcleithrum in lateral view, from BMNH P.56491.

The endoskeletal shoulder girdle is a single ossification, despite its complex shape. The mesocoracoid arch is well developed and dorsally is directed towards the posterior margin of the cleithrum. In other actinopterygians (except *Moythomasia* and *Acipenser*) the mesocoracoid arch is directed towards the anterior cleithral margin. The dorsal junction of the mesocoracoid arch with the scapular portion is drawn out posteriorly beyond the hind margin of the cleithrum (mscp, Fig. 126), as in *Moythomasia* (Fig. 131). This is the mesocoracoid process and it is also found in *Pteronisculus* (Jessen 1972: fig. 9).

The horizontal middle region of the girdle is produced anteriorly (apr, Fig. 129), as in many actinopterygians, and is perforated by two main foramina. The larger, hinder of these is the scapular foramen, that nearer the leading edge of the middle region the anterior scapular foramen. Both foramina occur in *Birgeria*, *Palaeoniscus*, *Acipenser*, *Amia*, *Elops* and *Salmo* (Jessen 1972). In addition a large coracoid foramen occurs at the junction of the mesocoracoid arch and the coracoid portion of the girdle; this is restricted to fossil actinopterygians.

The radial endoskeleton of the pectoral fin consists of a propterygium, three radials and a metapterygium. These articulate with an almost horizontally-orientated, elongate, glenoid fossa (gf, Fig. 128). The anterior or leading edge of the fin is slightly higher than the trailing edge and the fin is expanded in a horizontal plane much as in *Acipenser*, *Lepisosteus*, *Elops* and *Salmo*.

The propterygium is a short, ovoid ossification perforated by a canal. It is embraced by the bases of the marginal rays. The three radials (r, Fig. 137) are a little longer than the propterygium; they are hourglass-shaped, perichondral ossifications. The metapterygium is over twice as long as the radials and supports three short preaxial radials. No distal radials have been observed, but these may have been cartilaginous, as in *Polypterus*, or covered by the proximal ends of the lepidotrichia, as in *Pteronisculus* (Nielsen 1942: 235).

There appear to be 18–20 pectoral rays, the principal of which are only articulated distally. Along the leading edge the terminations of the lepidotrichia alternate with fringing fulcra, as in *Canobius*, *Mesopoma* and *Rhadinichthys*.

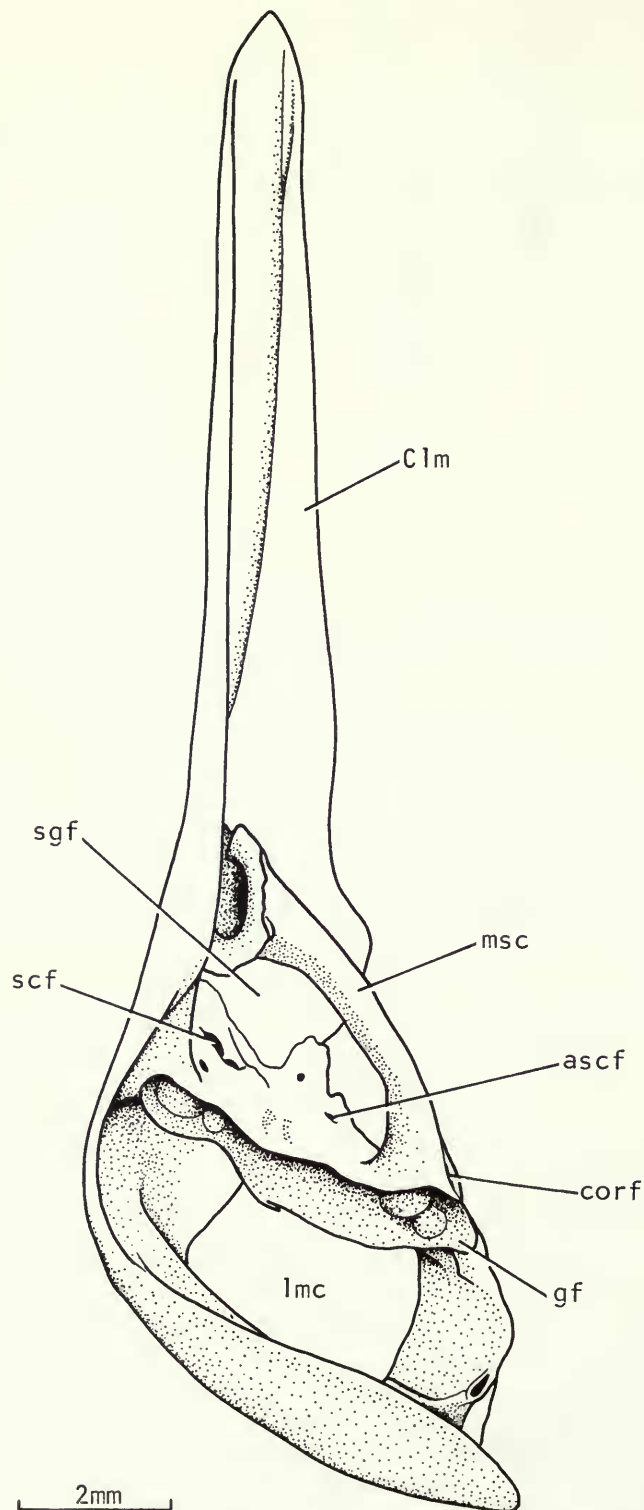


Fig. 128 *Mimia toombsi* Gardiner & Bartram. Left cleithrum and endoskeletal shoulder girdle in posterior view, from BMNH P.53245.

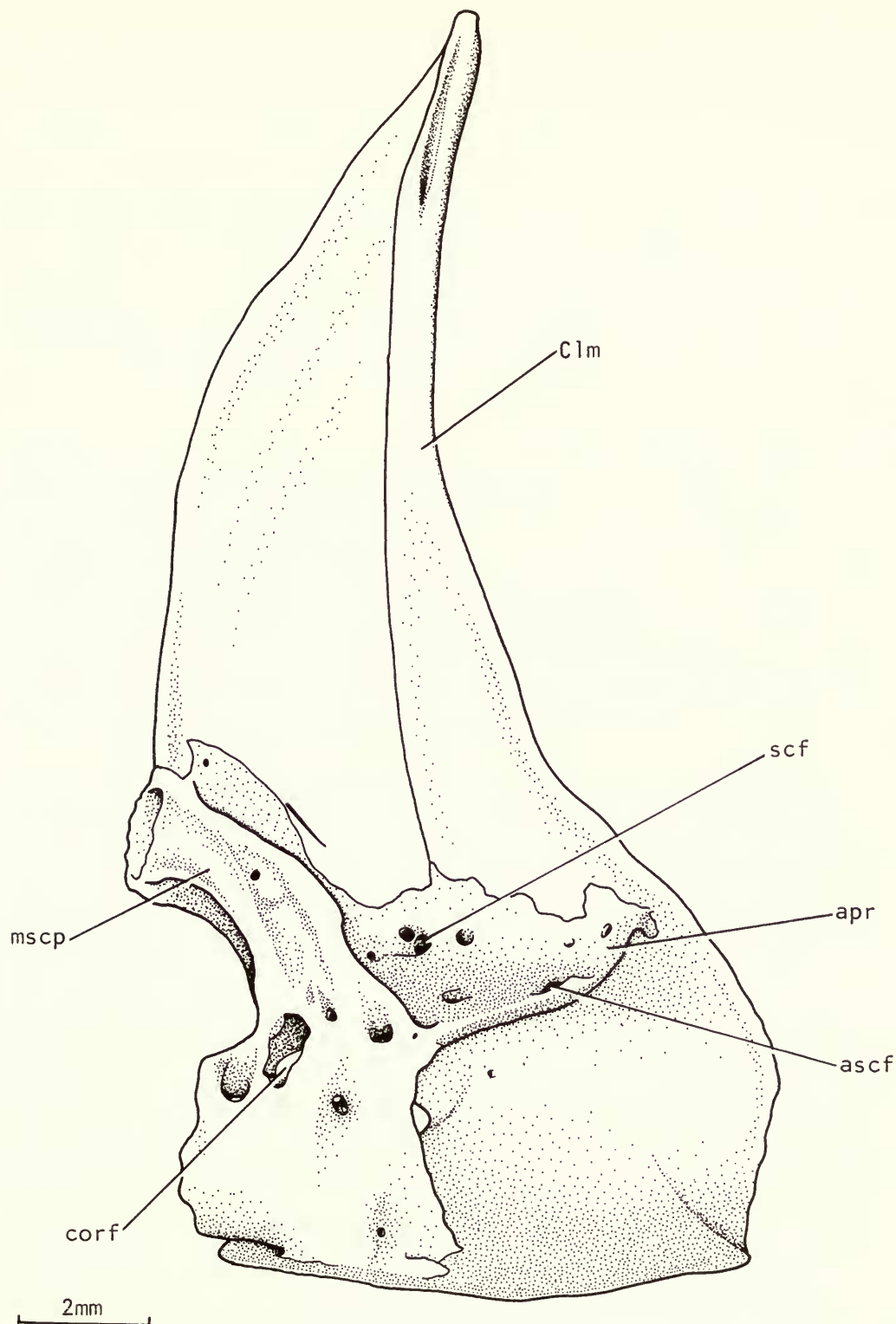


Fig. 129 *Mimia toombsi* Gardiner & Bartram. Left cleithrum and endoskeletal shoulder girdle in medial view, from BMNH P.53245.

Moythomasia durgaringa

The pectoral girdle is very similar to that of *Mimia*. The few differences include the size and shape of the postcleithrum and interclavicle, and minor differences in the endoskeletal girdle and fin construction.

The postcleithrum has a much longer, pointed, dorsal peg with an anteriorly-directed process (Fig. 133). The interclavicle is proportionally larger than in *Mimia* and ventrally has two distinct ornamented areas (Figs 134, 135).

In several specimens there is a prominent rostrocaudally-running ridge on the ventral surface of the coracoid region, which marks the subdivision of the ventral fin musculature. A similar ridge is found in *Acipenser*, *Acrorhabdus*, *Pteronisculus* (Aldinger 1937, Nielsen 1942), *Perleidus*, *Pachycormus* and *Elops* (Jessen 1972).

The pectoral fin has a propterygium to which the first three lepidotrichia are attached (Fig. 136) and the first ray is ornamented with longitudinal ridges of ganoine. The remainder of the fin is supported by four radials and a metapterygium. There are 19–24 lepidotrichia, and fringing fulcra occur along the anterior margin, as in *M. nitida* (personal observation).

Shoulder girdle and pectoral fin: discussion

1. Dermal bones of shoulder girdle

Primitive actinopterygians show a series of four paired bones plus a median interclavicle, whereas sarcopterygians have five paired bones and an interclavicle. The actinopterygian shoulder girdle differs from that of other osteichthyans in having the cleithrum overlapped dorsally by the supracleithrum. Rosen *et al.* (1981) have argued that this is the primitive osteichthyan condition. In osteolepiforms, actinistians, porolepiforms and dipnoans an extra element, the anocleithrum, separates the supracleithrum from the cleithrum; Jarvik (1944b) has hypothesized this to be the primitive osteichthyan condition. Jarvik further suggested that the actinopterygian condition had been arrived at by regression of the anocleithrum. Rosen *et al.* (1981), in contrast, suggested that the anocleithrum developed from the scale-like actinopterygian postcleithrum, and proposed that the incorporation of the postcleithrum (= anocleithrum) as a functional unit in the girdle is a synapomorphy for *Eusthenopteron* and other sarcopterygians.

There is little doubt that the actinopterygian postcleithrum has been derived from the scale row immediately behind the girdle. In *Mimia*, for example, its articulation with the supracleithrum is by an expanded peg, homologous with that on other scales. Further, the postcleithrum in *Polypterus* (Jarvik 1944b), *Pygopterus* and *Boreosomus* is little more than the most dorsal member of a modified scale row. A pair of scale-like postcleithra occurs in *Scomber*, but primitive teleosts have three. A postcleithrum is absent in some teleosts and palaeoniscids (*Stegotrachelus*, *Cornuboniscus*, *Watsonichthys*), including *Cheirolepis*, where the scales are very small and without peg-and-socket articulations. The absence in *Cheirolepis* is thought to be primitive, as are the small scales devoid of peg-and-socket articulations. Pearson & Westoll (1979) described a postcleithrum in *Cheirolepis*, but re-examination of their material (including BMNH P.41310, P.36061) has failed to convince me of its presence.

A large scale-like extracleithrum is found in fossil actinistians (cf. *Rhabdoderma*, Forey 1981: fig. 7) and is regarded as synapomorphous for that group.

Elsewhere a dermal shoulder girdle is found in acanthodians and placoderms and many attempts have been made to homologize their various dermal elements with those of living forms (Jaekel 1899, 1906; Dean 1907; Jarvik 1944b; Stensiö 1944, 1947, 1959). Despite these attempts a separate nomenclature is usually employed for the dermal bones of acanthodians (Miles 1973b, Denison 1979) and another for placoderms (Denison 1978).

In acanthodians the shoulder girdle is strengthened by dermal plates and spines both ventrally and laterally. These are best developed in the *Climatiidae* and *Diplacanthidae* but are also present in the *Gyracanthidae*. Dermal plates are wanting in the *Ischnacanthidae* and *Acanthodidae* (Miles 1973b). The dermal plates, where present, are in two series. Ventrally there is a median unpaired plate (median loral plate) in *Brachyacanthus*, *Parexus*, *Vernicomacanthus* and *Lupopsyrus*, and two median unpaired plates in *Climatius* (Miles

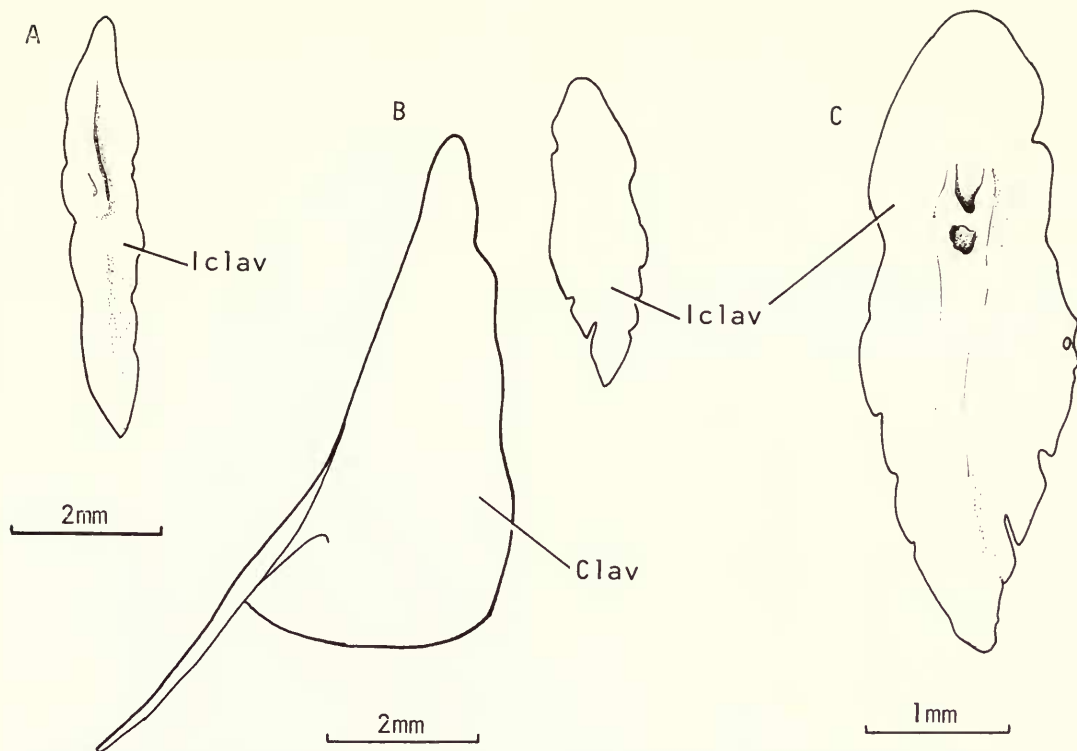


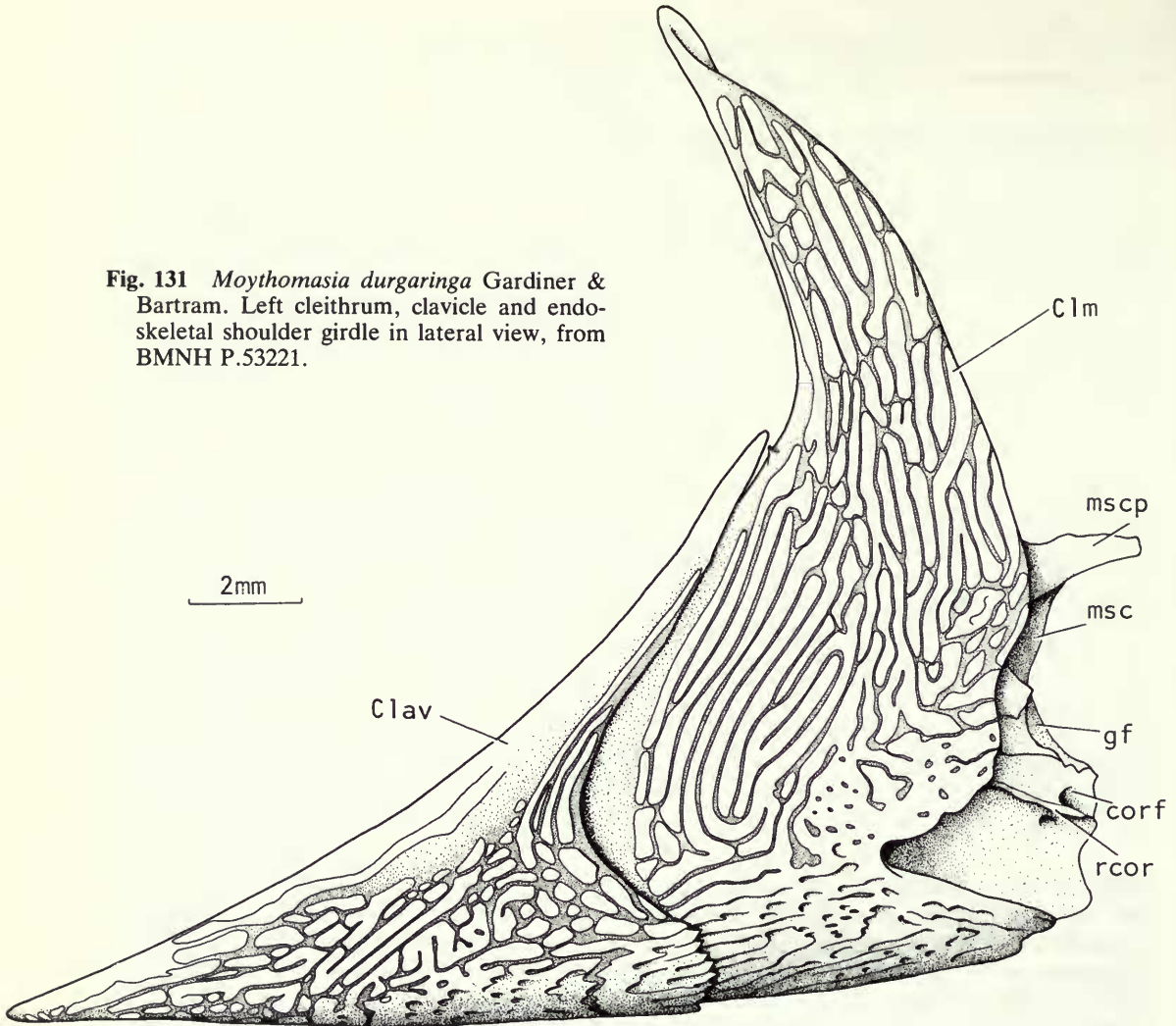
Fig. 130 *Mimia toombsi* Gardiner & Bartram. Interclavicle in (A), (C) dorsal and (B) ventral views. (B) Left clavicle in dorsal view. (A) from BMNH P.56473; (B), (C) from BMNH P.56484.

1973b). Ventrolaterally, on either side of the median plate, is a pair of so-called pinnal plates in *Erriwacanthus*, *Vernicomacanthus*, *Parexus*, *Lupopsyrus*, *Sabrinacanthus*, *Ptomacanthus*, *Euthacanthus* and *Gyracanthus*. There are two such pairs in *Brachyacanthus* and *Gyracanthides* and three in *Climatius* (Miles 1973b). The pinnals of *Erriwacanthus*, *Vernicomacanthus* and *Sabrinacanthus* all have extensive ascending laminae.

Dean (1907) suggested that these plates in acanthodians are homologous with the osteichthyan interclavicle and clavicle, whereas Jaekel (1899) homologized them with the cleithrum. Miles (1973b: 205) maintained that, although it was possible to compare the ventral bones in climatiiforms with those of the osteichthyan girdle, he found such comparisons imprecise; he concluded that the ventral shoulder-girdle plates of acanthodians and osteichthyans had been independently acquired and that the similarities between them were fortuitous. He also concluded (1973b: 162) that there was little possibility of the dermal plates of acanthodians and placoderms being homologous, and so found it necessary to introduce a new terminology for the plates in acanthodians. He came to these conclusions because he assumed that the generalized climatioid pattern comprised two loral plates and three or four paired pinnal plates, as in *Climatius*. If, however, a single median plate and one pair of lateral plates, as in *Vernicomacanthus*, is the primitive acanthodian condition then the correspondence with the osteichthyan interclavicle and clavicles is far more exact. Moreover, the posterior pinnal plate in *Brachyacanthus* and *Climatius* may be homologous with the spinal plate in ptyctodonts and other placoderms.

Placoderms resemble osteichthyans in having several lateral dermal plates associated with the shoulder girdle and it is probable that it is the short girdle that is primitive for placoderms (Denison 1975), not the elongated thoracic shield of early arthrodires as argued by Gross (1954). The former point of view is supported by the cladograms of placoderm interrelationships put

Fig. 131 *Moythomasia durgaringa* Gardiner & Bartram. Left cleithrum, clavicle and endoskeletal shoulder girdle in lateral view, from BMNH P.53221.



forward by Miles & Young (1977) and Young (1980), in which ptyctodonts are considered the sister-group of all other placoderms.

Miles & Young (1977) proposed that the primitive placoderm possessed median dorsal, anterior dorsolateral, anterior lateral, interolateral, spinal, anterior ventrolateral and anterior median ventral plates. Ptyctodonts conform to this pattern apart from the absence of the interolateral.

Jaekel (1906) and Stensiö (1959) homologized the anterior median ventral, anterior ventrolaterals and anterior laterals of arthrodires with the interclavicle, clavicles and cleithra of osteichthyans. Their comparisons would, however, have been more exact had they substituted ptyctodonts for arthrodires. If ptyctodonts are the most primitive placoderms and this sort of outgroup comparison is meaningful, it follows that additional plates must have been added to the thoracic shield within the placoderms (see Young 1980: 69). Furthermore, the anterior edge of the cleithrum (anterior lateral) turns inwards to form a postbranchial lamina in both ptyctodonts and *Romundina* (Ørvig 1975: fig. 2A), much as in osteichthyans.

Stensiö (1959) further homologized the anterior dorsolateral with the osteichthyan post-temporal because of the contact that both were supposed to have made with the

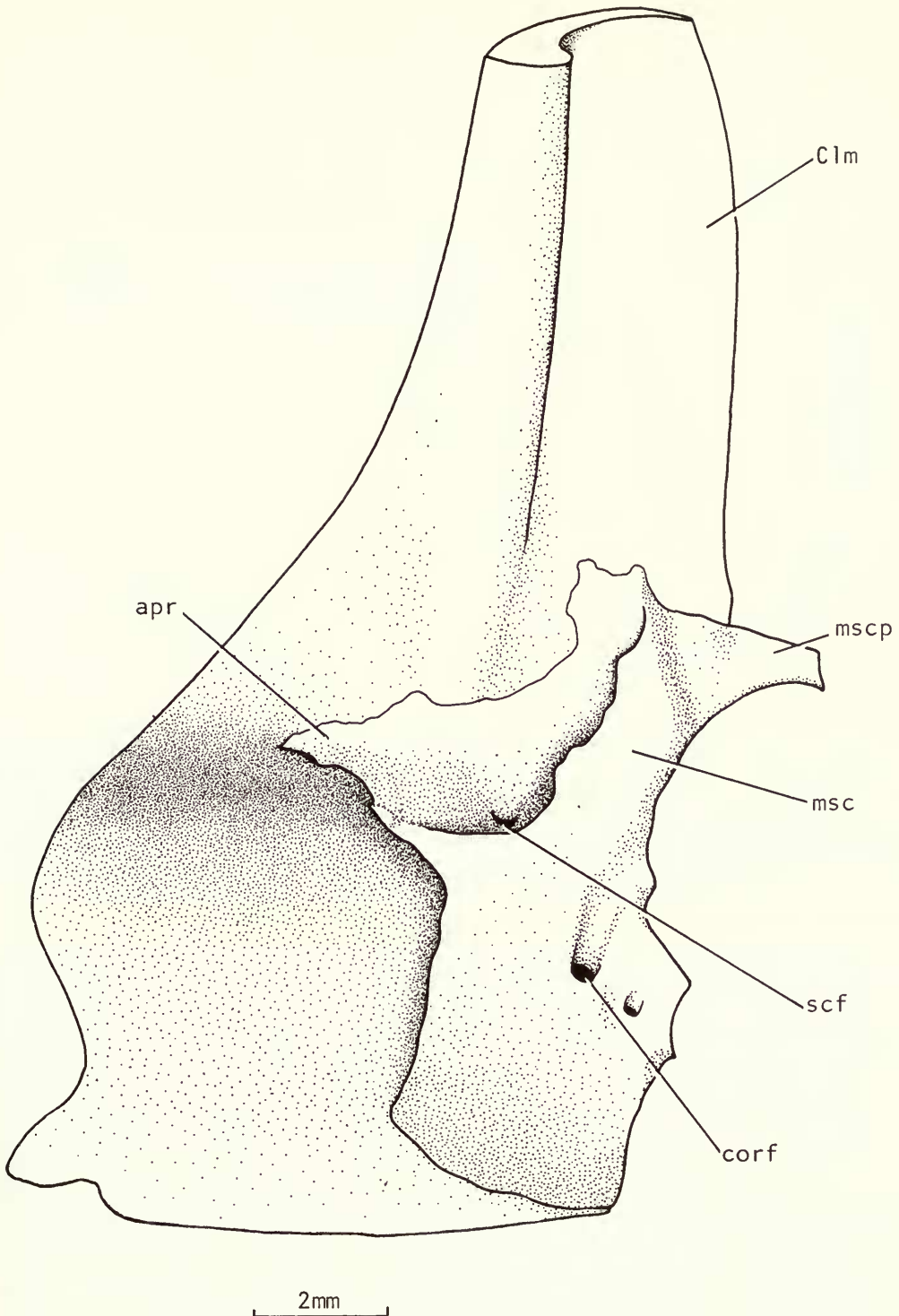


Fig. 132 *Moythomasia durgaringa* Gardiner & Bartram. Right cleithrum and endoskeletal shoulder girdle in medial view, from BMNH P.53218.

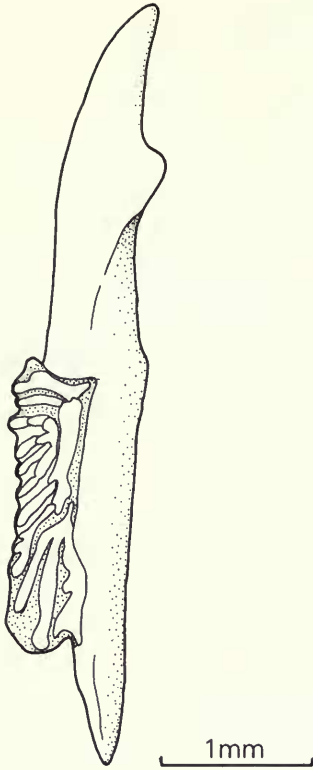


Fig. 133 *Moythomasia durgaringa* Gardiner & Bartram. Right postcleithrum in lateral view, from BMNH P.53256.

neurocranium. But the anterior dorsolateral separates the anterior lateral (cleithrum) and median dorsal and is overlapped by both of these elements.

From this survey I conclude that the presence of ventral dermal plates on the shoulder girdle is synapomorphous for a group including acanthodians, placoderms and osteichthyans, that the cleithrum is a synapomorphy of placoderms and osteichthyans and the anocleithrum a synapomorphy of sarcopterygians.

2. Endoskeletal girdle

The actinopterygian shoulder girdle is tripartite and characterized by a middle region with an anterior process (Jessen 1972). The dorsal process is termed the mesocoracoid arch and the dorsomedial muscles of the fin pass beneath it. The anterior diazonal nerves enter the canal formed by this arch and the middle region from in front, and the ventral branches pass through a foramen in its floor. This foramen is called the scapular foramen or posterior canal (Jessen 1972). A separate coracoid foramen for at least one of the ventral branches of a diazonal nerve passes through the medial surface of the scapulocoracoid near the base of the mesocoracoid arch. A separate anterior scapular foramen transmits a branch of the pectoral vein (Jessen 1972). A well-developed anterior process is found in actinopterygians, including *Mimia*, *Moythomasia*, *Palaeoniscus*, *Lepisosteus*, *Amia*, *Caturus*, *Hypsocormus* (Jessen 1972) and teleosts. Pearson & Westoll (1979) have suggested that a middle region is present in *Cheirolepis*, but I am unable to confirm this; however, I have seen remnants of what I interpret as a mesocoracoid arch in BMNH 19428 and P.4345. The shoulder girdle is ossified in one piece (including the mesocoracoid arch) in several actinopterygians, including *Mimia*, *Pachycormus*, *Pholidophorus* and *Leptolepis*. In primitive living teleosts, however, it is ossified in three parts, a ventral coracoid, a middle region or scapula and a dorsal mesocoracoid (e.g. *Cyprinus*, *Mormyrus*, *Salmo*, *Elops*). In more advanced teleosts the mesocoracoid arch is lost.

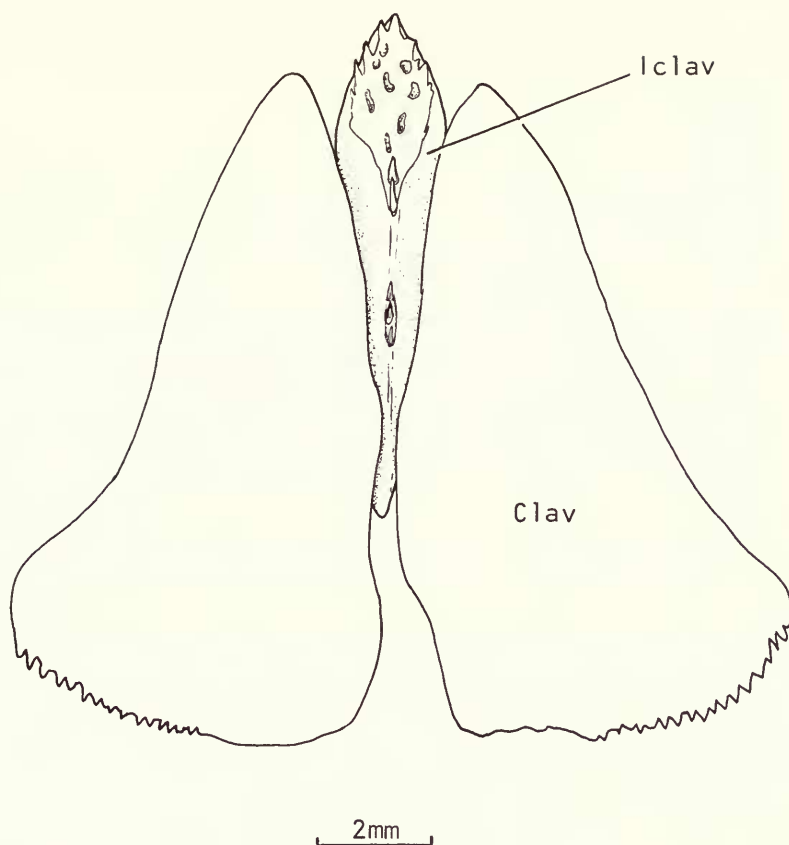


Fig. 134 *Moythomasia durgaringa* Gardiner & Bartram. Clavicles and interclavicle in ventral view, from BMNH P.53219.

Ventrally the tripartite girdle is attached to the clavicle by the anterior coracoid process which forms a canal for the marginal and ventral fin muscles, the supracoracoid foramen. This process and canal are missing in *Amia* and several teleosts (e.g. *Anguilla*).

Both the coracoid process and mesocoracoid arch are missing in *Polypterus* and in common with some teleosts there are two ossifications, the scapula and coracoid. The canal through the girdle of *Polypterus* is thought to be homologous with the coracoid foramen (= posterior canal of Jessen 1972) of other actinopterygians, since it transmits ventral branches of the fourth spinal nerve and posterior arteries and veins of the fin. This canal or foramen passes between the coracoid and scapula in *Polypterus* but through the scapula in teleosts.

A tripartite girdle similar to that of actinopterygians is also found in osteolepiforms (Janvier 1980) and fossil dipnoans (Rosen *et al.* 1981), where the supraglenoid foramen is homologous with the upper muscle canal of Jessen, the supracoracoid foramen with the lower muscle canal and the dorsal buttress with the mesocoracoid arch. The characteristic actinopterygian middle region is represented by the small posterior buttress (Patterson 1982), but unlike actinopterygians there are no apparent nerve foramina. Actinistians on the other hand resemble Recent dipnoans in having an unfenestrated scapulocoracoid which in *Rhabdoderma* (Forey 1981) is represented by a triangular bone resting against the inner surface of the cleithrum.

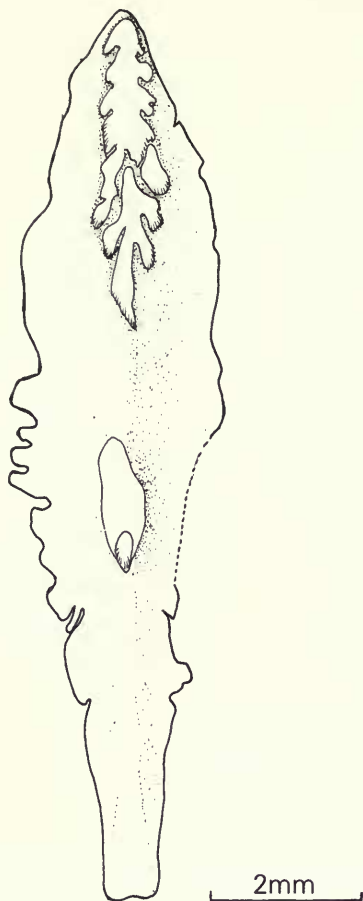


Fig. 135 *Moythomasia durgaringa* Gardiner & Bartram. Interclavicle in ventral view, from BMNH P.56502.

In primitive tetrapods the scapulocoracoid is also ossified in a single piece (e.g. *Eogyrinus*, *Eryops*, *Cacops*) and the supraglenoid buttress is homologous with the osteolepiform and dipnoan dorsal buttress and the actinopterygian mesocoracoid arch (Goodrich 1930: 174). In frogs and many amniotes there are two ossifications, referred to as the scapula and coracoid. In yet other amniotes (*Pareiasaurus*, *Procolophon*, dicynodonts, cynodonts, monotremes) there are three ossifications, with the additional element being referred to as the procoracoid. Thus extant tetrapods and many fossil amniotes resemble *Polypterus* and living teleosts in the retention of sutures between the cartilage-bones in the adult pectoral girdle.

Large size and anterior extent of the middle region of the shoulder girdle characterize actinopterygians and the scapular foramen and anterior scapular foramen are synapomorphous for actinopterygians. The tripartite girdle with its supraglenoid foramina is synapomorphous for osteichthyans. We may also infer that the primitive number of ossifications in the osteichthyan endoskeletal girdle is three.

In chondrichthyans and acanthodians (*Ptomacanthus* Miles 1973b) the two halves of the girdle are connected by cartilage or fibrous tissue, and this may be the primitive gnathostome condition.

In *Acanthodes* (Miles 1973b) the scapulocoracoid is perichondrally ossified in three pieces, a large scapulocoracoid (with a hollowed coracoid plate), a small suprascapula and a procoracoid which articulated with the scapulocoracoid and supported the pectoral fin spine. A well-defined canal passes through the scapulocoracoid and opens externally beneath the glenoid fossa via the coracoid foramen. This canal is presumed to have transmitted diazonal nerves and vessels.

There are two such canals in *Diplacanthus*, whereas in *Sabrinacanthus* (Miles 1973b) there are numerous fine foramina ramifying through the posteroventral region of the scapulocoracoid, as in some placoderms.

In chondrichthyans (e.g. *Hexanchus*, *Pristiurus*, *Chimaera*) there is usually a single, internal coracoid foramen for the diazonal nerves, but this soon divides and opens externally above and below the glenoid fossa. The coracoid foramen is also seen in *Acipenser* and other actinopterygians, as well as many tetrapods, and is consequently considered to be a primitive gnathostome feature. The external upper opening is called the supraglenoid foramen, but this is not homologous with the similarly-named canal in osteichthyans (see p. 378). The coracoid region expands immediately below the pericardium and there is a distinct coracoid fossa beneath the glenoid fossa, as in *Acanthodes*, for the ventral fin musculature.

There is considerable variation in the pectoral endoskeleton of placoderms and in the presumed advanced forms the scapulocoracoid is a low structure lacking a prominent scapular blade (arthrodires). Pseudopetalichthyids, rhenanids and arthrodires (Broili 1933, Stensiö 1959, Young 1980) have an extensive anteriorly-directed coracoid process and arthrodires have an elongated glenoid fossa. The long, low scapulocoracoid of arthrodires is crossed by a series of diazonal nerves and segmented vessels. An extensive coracoid process is seen elsewhere in acanthodians (*Sabrinacanthus*), chondrichthyans and actinopterygians and is probably primitive, as Miles (1973b) suggested.

A scapular process is found in *Pseudopetalichthys*, certain rhenanids (*Brindabellaspis*, *Jagorina*) and ptactodonts. This is regarded as a primitive gnathostome feature as suggested by Young (1980: 51).

In ptactodonts there is a canal for the ventral fin musculature, bounded externally by the clavicle (anterior ventrolateral plate, Miles & Young 1977). This canal is homologous with the supracoracoid foramen of osteichthyans and is inferred to have been formed by a plate of dermal bone bridging the coracoid fossa. In osteichthyans it is bounded by the cleithrum, except in *Acipenser* where the clavicle forms its anterior margin. In *Rhynchodus* (Stensiö 1959: fig. 75) the identical canal has a rim of perichondral bone posteriorly. A similar ventral fossa also occurs in the palaeacanthaspids *Romundina* (Ørvig 1975: pl. 5) and *Palaeacanthaspis* (Stensiö 1944: fig. 9), but here it is closed anteriorly by perichondral bone. This canal or fossa is absent in other placoderms but nevertheless is regarded as a synapomorphy of a group containing placoderms and osteichthyans. In ptactodonts the endoskeletal girdle and glenoid fossa project posteriorly beyond the dermal girdle, much as in actinopterygians, and the pectoral fin is similarly orientated in both groups.

A coracoid foramen has been recorded in *Brindabellaspis* (Young 1980) and *Romundina* (Ørvig 1975: pl. 4, dzv).

3. Pectoral fin

The pectoral fin of actinopterygians is characterized by having a propterygium (Rosen *et al.* 1981), a first radial which is short, broad and strongly articulated. In *Mimia*, *Moythomasia*, *Palaeoniscus*, *Pteronisculus*, *Acipenser*, *Lepisosteus* and most actinopterygians (Patterson 1982) the propterygium is perforated by a canal which in living forms conducts nerves and vessels (Jessen 1972). A perforated propterygium is an actinopterygian character (Patterson 1982).

A well-developed propterygium is also found in *Cheirolepis* (Ra₂, Ra₃ of Pearson & Westoll 1979: fig. 13) where it is clasped by four lepidotrichia (BMNH P.6096a). There is no evidence of a propterygial canal and in this respect *Cheirolepis* resembles *Polypterus*.

Rosen *et al.* (1981) have interpreted actinopterygian paired fin structure as a transformation of a metapterygial fin into a propterygial type. Certainly, pectoral metapterygial elements are still to be found in such primitive members as *Cheirolepis* (personal observation), *Mimia*, *Acipenser*, *Pteronisculus* and *Palaeoniscus* (Jessen 1972), and from a study of the development of *Polypterus* (Budgett 1902) much of the fin in this fish also appears to be metapterygial.

Two sets of radials usually occur in the pectoral fins of actinopterygians. Posteriorly in sturgeons and on the second radial of *Elops* there are three sets. The distal radials are triangular in shape and sit between the tips of the proximal radials in primitive forms.

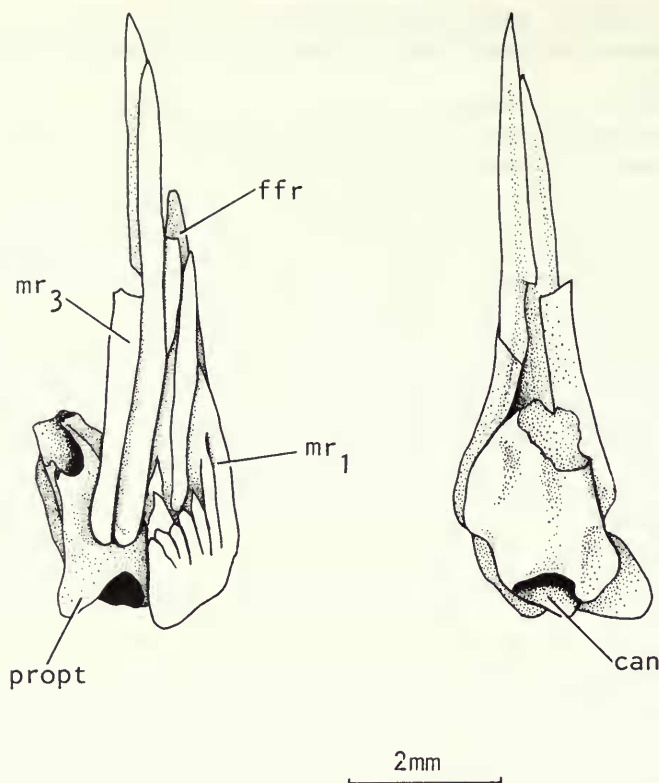


Fig. 136 *Moythomasia durgaringa* Gardiner & Bartram. Propterygium and leading fin-rays in external (left) and internal views, from Western Australian Museum no. 70.4.244 (holotype).

The bases of the marginal rays embrace the propterygium in actinopterygians and in *Moythomasia* and teleosts the first ray, at least, is attached to it. The first condition is considered synapomorphic for actinopterygians.

Pelvic girdle and fin

Mimia toombsi

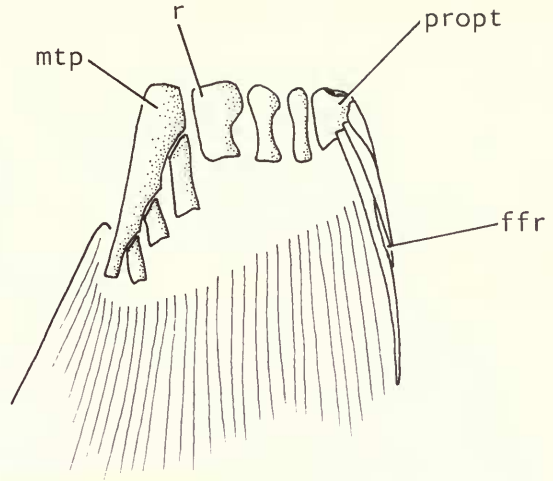
The fin is small and situated about midway between the pectoral and anal fins. Only one specimen contains traces of the pelvic girdle. The pelvic plate is smaller than in *Moythomasia* and is without an anteromedial process. No radials were observed. The fin consists of around 20 lepidotrichia.

Moythomasia durgaringa

The pelvic plate (Pg, Fig. 138) is a thin, triangular, perichondral ossification with a slender anteromedial process. Seven radials articulate with its posterior margin. The six anterior radials are of approximately the same size, but the seventh, the most posterior, is much larger and is presumed to represent the metapterygial axis. Seven radials have been recorded in *Acipenser* (Rosen *et al.* 1981: fig. 28B), eight in *Boreosomus* (Nielsen 1942), nine in *Scaphirhynchus* and as many as 14 in *Polyodon*. *Polypterus* has only four.

The pelvic fin is nearer to the anal than to the pectoral (cf. *M. nitida* Jessen 1968: fig. 4) and contains 18–20 jointed lepidotrichia. It bears fringing fulcra along its anterior edge.

Fig. 137 *Mimia toombsi* Gardiner & Bartram.
Reconstruction of the base of the right pectoral
fin in dorsal view, from several specimens.



Pelvic girdle and fin: discussion

The pelvic fin in actinopterygians appears to be constructed differently from the pectoral (Goodrich 1930), whereas in all other osteichthyans the two are similar in structure. Davidoff (1880) reasoned that this was because in actinopterygians the metapterygial skeleton of the pelvic fin had shifted inwards and been incorporated in the pelvic girdle. Rosen *et al.* (1981) revived Davidoff's theory as it offered an explanation of the observed similarity between the pelvic endoskeleton of chondrosteans and the metapterygium plus preaxial radials of chondrichthyans and because the alternative, that the chondrosteans possess the most primitive paired fins, violated the monophyly of osteichthyans and actinopterygians. They further reasoned that actinopterygians might not have a primary pelvic girdle.

In *Polyodon*, *Scaphirhynchus*, *Acipenser* and some palaeoniscids (Lehman 1966) there is a series of rod-like basal cartilages which are presumed to represent the segmental metapterygial skeleton. These fuse in most adults but may remain separate in some palaeoniscids and partially separate in *Scaphirhynchus*. Two rows of cartilages are joined to the outer surface of these internal cartilages, an inner row of elongate radials and a distal row of smaller triangular radials.

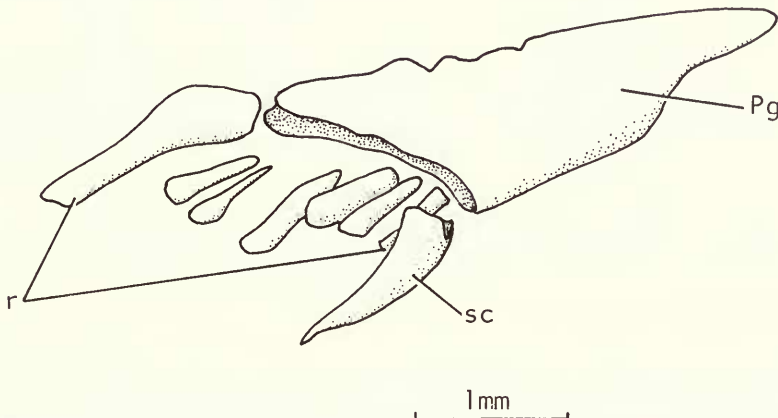


Fig. 138 *Moythomasia durgaringa* Gardiner & Bartram. Pelvic girdle and radials of the right side in dorsolateral view, from BMNH P.53236.

Two rows of radials also occur in *Polypterus*, *Pteronisculus*, *Boreosomus*, *Pygopterus* and many other palaeoniscids, and also in *Lepisosteus* and *Amia*, but in teleosts there is only a single series. There are some 14 proximal radials in *Polyodon*, ten in *Pteronisculus*, nine in *Scaphirhynchus*, eight in *Boreosomus*, seven or eight in *Acipenser* and four in *Polypterus*. In *Lepisosteus*, *Amia* and primitive teleosts the radials are reduced to never more than three small nubbins, and in many teleosts there is no trace of radials.

I conclude, like Patterson (1982), that a pelvic plate and two series of radials are synapomorphous for actinopterygians.

Median fins

Mimia toombsi

The dorsal fin lies in the posterior half of the body opposite the anal fin (Fig. 145). Remnants of the endoskeleton of the median fins are found in several specimens, but owing to the post-mortem folding and twisting of the body exact relationships of individual ossifications are difficult to determine. Nevertheless, both dorsal and anal fins appear to be supported by a single series of radials.

In the dorsal fin the few anterior radials are rod-like; posteriorly the fin is supported by three compound radial plates (rpl, Fig. 124). These posterior plates correspond in part to the single axonost plates described in *Pygopterus*, *Pteronisculus*, *Birgeria* and *Australosomus* (Aldinger 1937, Nielsen 1942, 1949). The dorsal fin has 28–36 branched, segmented lepidotrichia and on the leading edge fringing fulcra alternate with the lepidotrichial endings.

The anal fin is supported by seven long radials which are expanded distally and there is a single complex radial plate posteriorly. This radial plate (rpl, Fig. 124) has lateral wing-like extensions proximally and these are perforated by a small foramen. A much larger foramen passes through the centre of the radial plate. The anal fin is made up of 30–40 branched, segmented lepidotrichia.

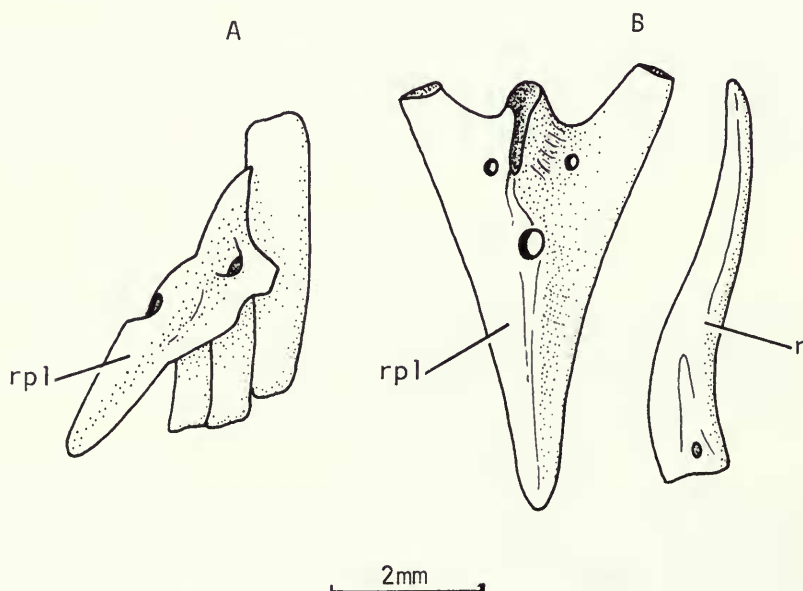


Fig. 139 (A), anal radials and anal radial plate of *Mimia toombsi* Gardiner & Bartram in right lateral view, from Western Australian Museum no. 70.4.245 (holotype). (B) *Moythomasia durgaringa* Gardiner & Bartram, anal radial plate in dorsal view, anal radial (right) in lateral view, from BMNH P.53218.

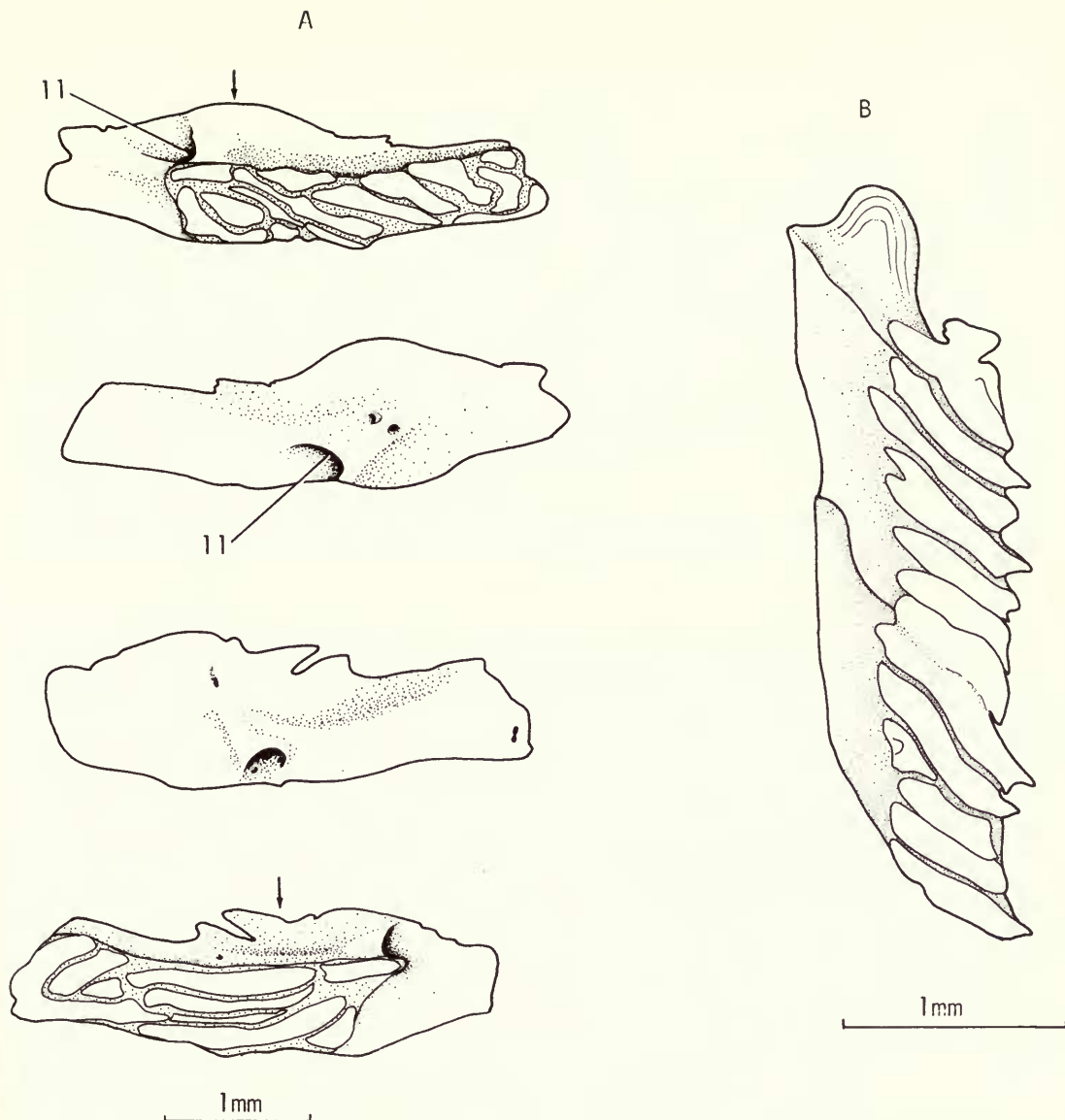


Fig. 140 *Mimia toombsi* Gardiner & Bartram. (A), two lateral line scales in lateral and medial views (arrow marks anterior), from BMNH P.56497. (B), two articulated, anterior trunk scales, from BMNH P.56495.

The caudal fin is deeply cleft and inequilobate and the lepidotrichia are closely set, branched and jointed. There are some 50 or more lepidotrichia and along the ventral margin the lepidotrichial endings alternate with fringing fulcra.

Moythomasia durgaringa

The dorsal and anal fins are opposite to one another, nearer to the tail than the head. The dorsal fin is slightly longer than that of *Mimia* with around 40 lepidotrichia, but the anal fin is of comparable size (30–35). A similar radial plate is present at the rear of the anal fin (rpl, Fig. 139); it only differs from that of *Mimia* in the possession of a posteriorly-directed distal flange.

The caudal fin has around 80 lepidotrichia and the ventral margin supports fringing fulcra.

Median fins: discussion

1. Dorsal and anal fins

Most actinopterygians have a single dorsal and anal fin, but many teleosts also have an adipose dorsal fin which may be supported by actinotrichia. Other teleosts may have as many as three dorsal and two anal fins (*Gadus*) and a continuous dorsal fin is seen in many palaeoniscids (e.g. *Tarrasius*) and teleosts (gymnotids, anguillids).

The dorsal and anal fins are supported by a series of parallel radials which are often arranged in three series (each radial is three-segmented). The radials beneath the dorsal and anal fins are three-segmented in chondrosteans, many palaeoniscids (*Birgeria*, *Pteronisculus*, *Boreosomus*), *Lepisosteus*, *Amia* and several teleosts (e.g. osteoglossids, cyprinids, salmonids, esocids), and are two-segmented in *Tarrasius*, *Australosomus* and many other teleosts (gadids, characinids, clupeids; Bridge 1896). In *Polypterus* the dorsal fin is supported by a single series but in the anal fin all the radials, apart from the first, are in two parts. The lepidotrichia clasp the ends of the radials forming modified ball-and-socket joints in neopterygians, where the distal radials are spherical. Posteriorly some of the distal dorsal and anal radials are compounded into an axonost or radial plate in *Mimia*, *Pteronisculus*, *Birgeria*, *Pygopterus* and *Australosomus* (Nielsen 1942, 1949).

Primitively the fin-rays far exceed the radials in number, but in neopterygians, haplolepidids, perlepidids, *Bobasatrania*, *Luganoia* and *Platysagum* (Patterson 1973) the number of dorsal and anal fin-rays is equal to that of their supports.

2. Caudal fin

The caudal fin in actinopterygians is primitively heterocercal, although a small epaxial lobe occurs near the tip of the tail in several adult palaeoniscids (*Cheirolepis*, *Palaeoniscus*, *Paramblypterus*) and is present in the ontogeny of Recent forms where it is supported by actinotrichia. In palaeoniscids it is supported by small lepidotrichia. Large epaxial fin-rays are developed in saurichthyids, amiids, pholidopleurids, pycnodonts, pachycormids and other teleosts (excluding pholidophorids). If the published phylogenies are correct (Patterson 1973, 1977a) they must have been independently developed on at least six occasions.

In living chondrosteans there is a series of median epurals lying above the neural arches of the tail; these are believed to be serial homologues of the supraneurals (Patterson 1973).

In advanced actinopterygians the tail is homocercal and in halecomorphs and teleosts the epaxial fin-rays are supported by a few epurals. There are seven epurals in pachycormids, six in *Australosomus*, four or five in *Amia* and three or fewer in living teleosts (Patterson 1973). In pycnodonts the epaxial fin rays are apparently supported by the neural arches (Gardiner 1970).

In *Polypterus* there is no sure way of distinguishing between radials and epurals or between dorsal fin-rays and epaxial caudal rays; nevertheless in development there appear to be three epurals.

The hypaxial lobe in actinopterygians is supported mainly by the expanded haemal spines and hypurals. The hypaxial radials are reduced to small nubbins of bone or cartilage at the tips of these spines. Reduced hypaxial radials are found in palaeoniscids (*Pteronisculus*), chondrosteans, *Lepisosteus* and primitive teleosts. Radials are absent in *Polypterus* and the hypaxial lobe is supported solely by expanded haemal spines and hypurals. In actinopterygians the lepidotrichia clasp the spines and hypurals, as well as the radials where present.

Squamation

Mimia toombsi

The body is entirely covered with scales, which have a transverse course up to the inversion line at the base of the tail. There are approximately 75 transverse scale rows between the cleithrum and the line of inversion. Ridge scales completely clothe the dorsal margin and the area between the anal fin and the tail. There are ten ridge scales in front of the dorsal fin, two in front of the anal fin and eight between the anal and the tail. Those on the caudal fin form a rigid cutwater and extend right to the tip of the tail. All the ridge scales are median structures.

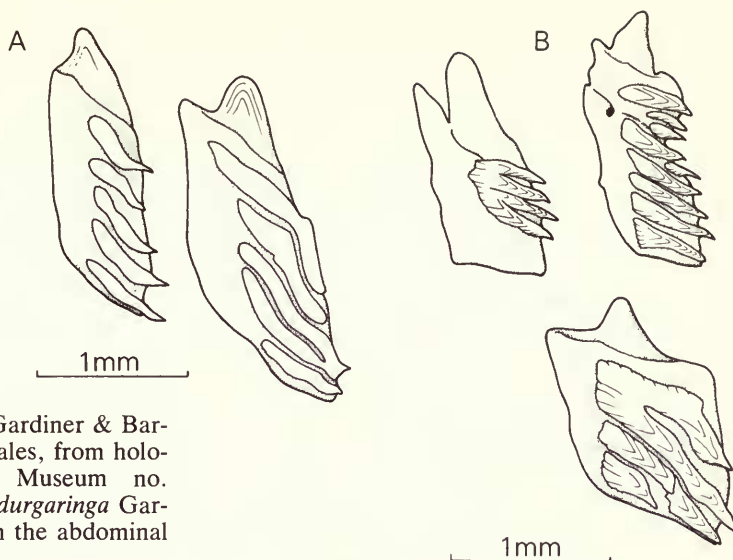


Fig. 141 (A), *Mimia toombsi* Gardiner & Bartram, posterior abdominal scales, from holotype, Western Australian Museum no. 70.4.245. (B), *Moythomasia durgaringa* Gardiner & Bartram, scales from the abdominal region, from BMNH P.56479.

The lobe of the pectoral fin is not scaly (cf. *Polypterus*, *Cheirolepis*), but the points of insertion of all the fins are marked by bands of much narrower scales.

The scales themselves have a deeply incised hinder margin and are ornamented with short ridges of ganoine which terminate posteriorly in sharp points. On the anterior trunk scales there are 7–10 stout ridges of ganoine, but posteriorly the number is reduced to four or five and near the base of the tail to one. They have well-marked peg-and-socket articulations, with the peg exhibiting growth lines (Pl. 2c). The lateral line scales are higher than broad and the lateral line canal enters the scale anteriorly at the junction of the peg with the anterodorsal ornamentation (Fig. 140A).

The scales have a diagonal long axis (see Gross 1966) and a reduced bony base (Fig. 143). Both dentinal tubules and dentine are apparently wanting and the cell spaces are exceptionally large. The ganoine layer is relatively thick and quite unlike that of any other actinopterygian. The ganoine is in the form of superposed generations which appear to have grown in an aberrant 'onion-skin' fashion without an accompanying layer of dentine. Judged by presumed younger individuals the ganoine first forms longitudinal ridges or blisters, completely separate from one another. These later fuse by the addition of further superficial layers of ganoine. The bony base consists of horizontal layers with contained cell spaces, canals of Williamson and canals for fibres of Sharpey.

Moythomasia durgaringa

There are far fewer transverse scale rows than in *Mimia*, with a scale count of between 44 and 48.

The scales are ornamented by ridges of ganoine which branch and anastomose. The ridges terminate posteriorly in up to 14 serrations on the more anterodorsal flank scales, but anteroventrally the scales have fewer serrations (eight or nine). Posteriorly the scales have five or fewer serrations. Behind the pelvic fin there is a pair of elongate, almost oval cloacal scales, equal in area to approximately three normal scales (BMNH P.53217).

Initially there are separate ridges of dentine and ganoine (Fig. 141B) and new ganoine and dentine are added between the ridges until the whole external exposed surface is ganoine-covered. The ganoine is single-layered over most of the scale, and this is presumed to be primitive (Schultze 1977). Superposed generations of buried ganoine are confined to the scale margins (Fig. 144) and to the edges of the primary ganoine ridges. The scales have a diagonal axis and a reduced bony base. The bony base contains cell spaces and canals for fibres of

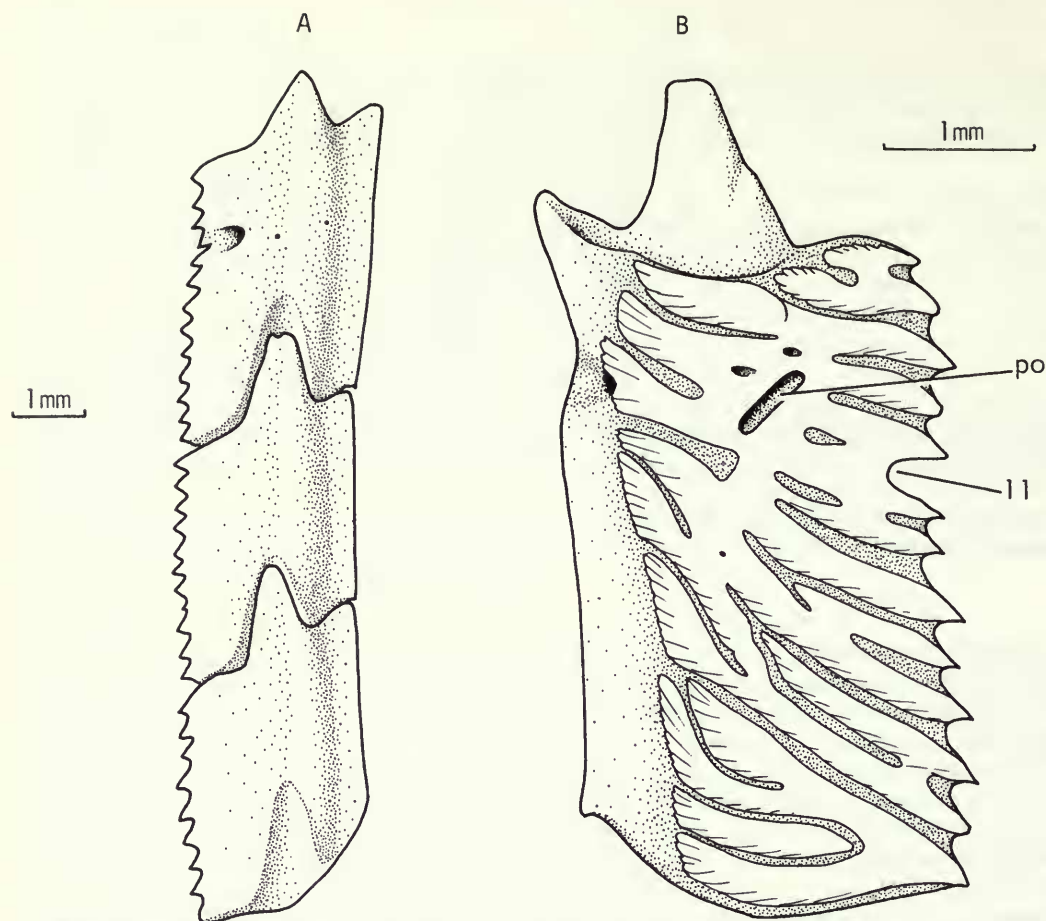


Fig. 142 *Moythomasia durgaringa* Gardiner & Bartram. (A), three scales in articulation, including the lateral line scale, medial view, from BMNH P.53221. (B), lateral line scale in lateral view, from BMNH P.53221.

Sharpey. Above the base is a horizontal vascular canal system from which the dentinal tubules pass upwards through the dentine layer.

The lateral line scales have surface pores and the ventral medial surface of the scales has a distinct depression for the articulatory peg of the scale immediately below it. The ornamentation is very variable and corresponds closely with that of *M. perforata* (Gross 1953: fig. 5).

Squamation: discussion

1. Scale structure

The scales of generalized actinopterygians are of the ganoid type in which the whole scale typically has an 'onion-skin' mode of growth, with new material being added concentrically to both the outer and inner surfaces. Bone is added to the base of the scale and ganoine to the surface, and the scale becomes thick and shiny. In advanced actinopterans the ganoine is pseudoprismatic (Ørvig 1967a, 1978) and in many teleosts is lost altogether.

In *Cheirolepis* (Gross 1967) the growth lines indicate that the layers of ganoine are added mainly to the anterior margin.

In *Polypterus* the superposed generations of buried ganoine are confined to the circumference (Meinke 1982: 371), but as in *Cheirolepis* they are most prominent on the anterior

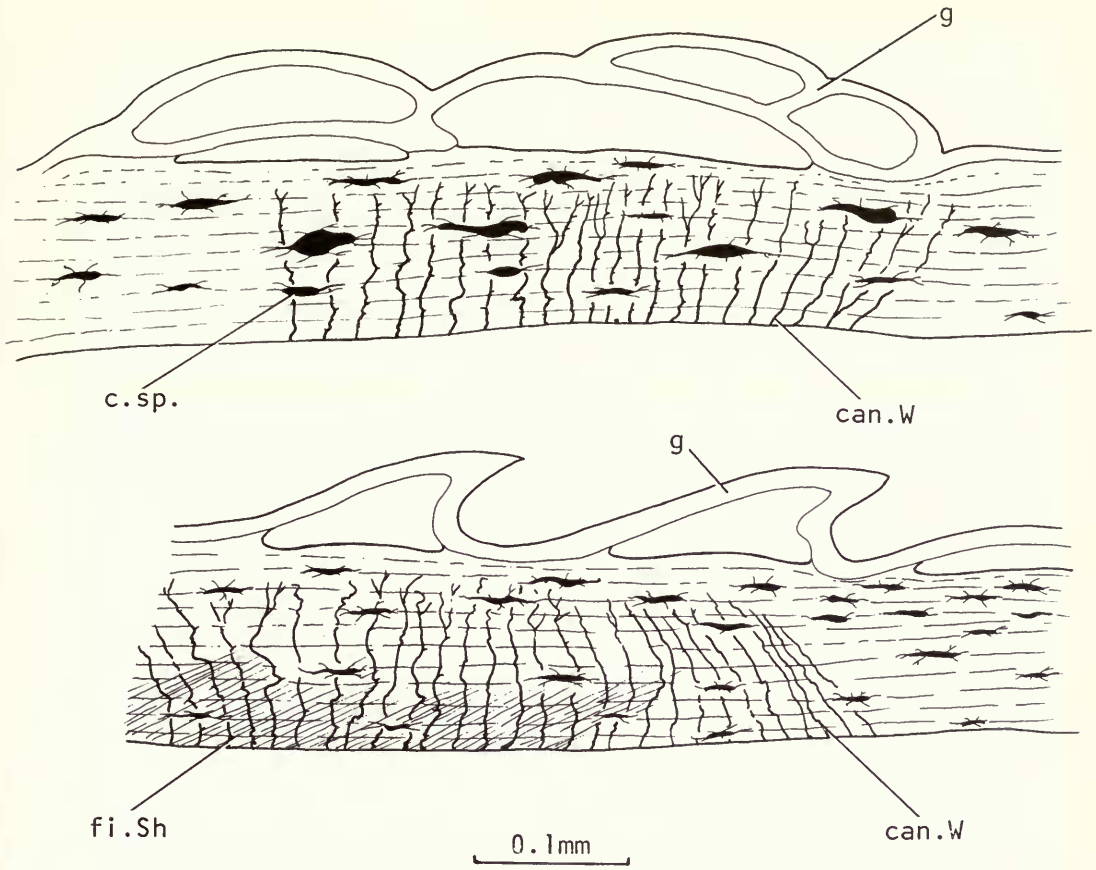


Fig. 143 *Mimia toombsi* Gardiner & Bartram. Vertical longitudinal sections through two flank scales. From BMNH P.56503.

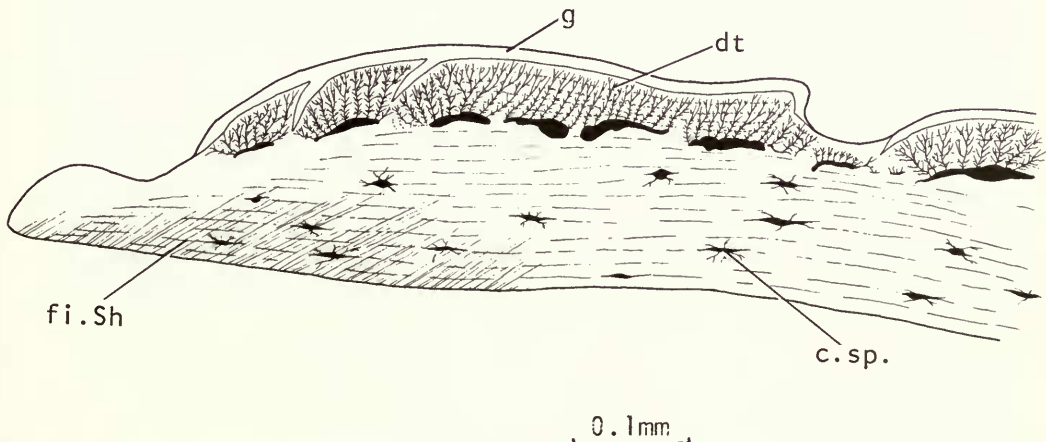


Fig. 144 *Moythomasia durgaringa* Gardiner & Bartram. Vertical longitudinal section through flank scale. From BMNH P.53221.

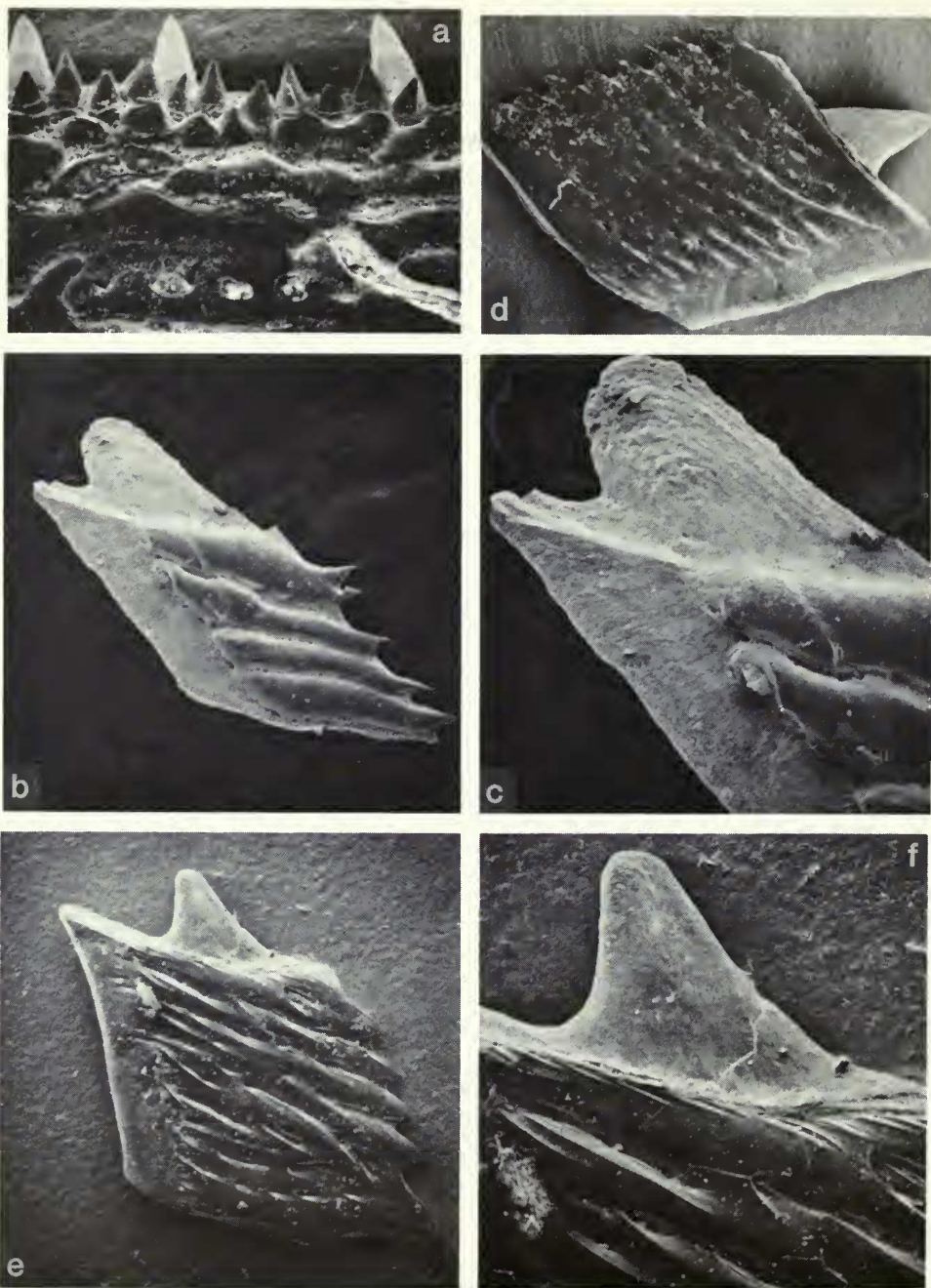


Plate 2 *Mimia toombsi* Gardiner & Bartram. (a) anterior end of dentary, from BMNH P.53252, $\times 30$. (b) posterior abdominal scale, from Western Australian Museum no. 70.4.245 (holotype), $\times 35$. (c) enlarged view of scale peg, same specimen, $\times 70$. Scanning electron micrographs.

Moythomasia durgaringa Gardiner & Bartram. (d) anterior flank scale, from Western Australian Museum no. 70.4.244, $\times 25$. (e) anterior scale, from BMNH P.53221, $\times 18$. (f) enlarged view of scale peg, same specimen, $\times 42$. Scanning electron micrographs.

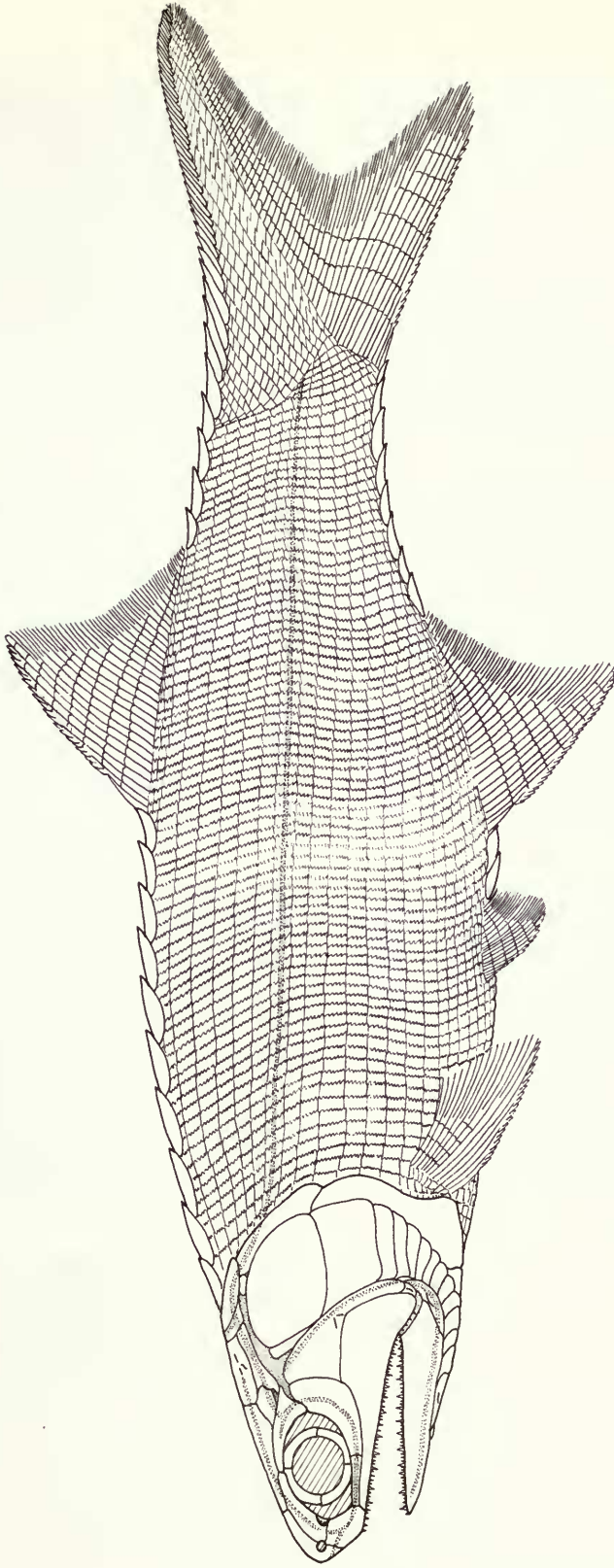


Fig. 145 *Mimia toombsi* Gardiner & Bartram. Restoration in lateral view.

margin. The scales of *Moythomasia* (Jessen 1968), like those of *Polypterus*, have a very thin layer of ganoine, with superposed generations of buried ganoine mostly confined to the scale margins. Thus the primitive actinopterygian scale seems to have grown by the addition of ganoine to the circumference rather than in the concentric 'onion-skin' fashion so typical of *Lepisosteus*. All primitive actinopterygian scales possess a superficial layer of ganoine which is said to be characteristic of actinopterygians (Schultze 1977, Patterson 1982). Slender peg-and-socket articulations between scales are also characteristic of actinopterygians but their absence from the scales of *Cheirolepis* is considered primitive. Nevertheless, the scales of *Cheirolepis* have a diagonal long axis and an anterodorsal process. A similar diagonal long axis and anterodorsal process characterize the scales of most actinopterygians (palaeoniscids, *Polypterus*, *Lepisosteus*) and is therefore considered synapomorphous for the group (Patterson 1982).

The scales of sarcopterygians never grow in the concentric 'onion-skin' fashion seen in actinopterygians. Instead they are of the cosmoid type with a superficial layer of enamel (Schultze 1977). Cosmine (dentine + enamel) is a hard tissue which encloses a complex pore-canal system. No living fish has either cosmine or a pore-canal system in the scales but the presence of both is regarded as a synapomorphy of rhipidistians and dipnoans (Rosen *et al.* 1981). The mesh canals linking the flask-shaped pore-canals have a horizontal partition in some osteolepiforms (Gross 1956) and this appears to be a specialization. Cosmine is missing from the scales of actinistians and tetrapods, but the scales of *Latimeria* do possess superficial tubercles which fuse to the scale surface. Separate tubercles occur above the scales in *Polypterus*, *Lepisosteus* and silurids. The scales of the dipnoan *Uranolophus* (Denison 1968, 1969) are characterized by Westoll-lines and superposed generations of tubercles.

The scales of euselachian chondrichthyans are typically placoid. Composite scales, however, occur in a Permian edestid holocephalian and the dorsal scales of 'Orodus' (Ørvig 1966) grew in 'onion-skin' fashion by the presumed concentric addition of dentine to the crown and fibrous bone to the base.

Placoderms are usually devoid of scales, but where they occur they are often small and rhomboidal (Miles & Westoll 1968).

The scales of acanthodians are small, closely fitting and made of concentric layers of bone and dentinal tissue. They had an 'onion-skin' mode of growth, similar to that in actinopterygians (Gross 1966, 1973). In the *Nostolepis* type the crown is mesodentine (Ørvig 1967b) and in the *Acanthodes* type it is dentine. In *Poracanthodes* there is a pore-canal system, but its architecture is quite unlike that of rhipidistians and dipnoans.

Within the gnathostomes this 'onion-skin' mode of scale growth is considered primitive.

2. Basal fulcra

The large paired or unpaired scale-like structures, preceding the bases of the median fins in primitive actinopterygians (Patterson 1982), are termed basal fulcra; they appear to be modified ridge scales. They are particularly well developed on the dorsal border of the tail in those primitive actinopterygians without elongate upper caudal fin-rays (most palaeoniscids, *Mimia* and chondrosteans). They are also present in *Dapedium*, *Lepisosteus*, *Eurycormus*, *Caturus*, *Ionoscopus* (Patterson 1973), parasemionotids and primitive teleosts. Basal fulcra are absent in *Polypterus* but this is presumed to be secondary and related to the acquisition of a diphycceral tail.

Basal fulcra may be found in front of all the unpaired fins, including both lobes of the caudal (*Cheirolepis*, *Elonichthys*, *Cornuboniscus*, *Mesopoma*, sturgeons, *Dapedium* etc.), or they may be missing from the anal (*Moythomasia*, *Phanerosteon*), or from both anal and dorsal

Plate 3 *Moythomasia durgaringa* Gardiner & Bartram, body scales. (a) mid-flank, $\times 27$. (b) basal fulcral, $\times 16$. (c) posterior flank, $\times 27$. (d) anterior flank, $\times 27$. (e) from base of tail, $\times 27$. (f) from tail, $\times 27$. (g) from base of anal fin, $\times 34$. (h) from base of pelvic fin, $\times 27$. Scanning electron micrographs, (a), (b), (d), (e), (f), (g) and (h) from BMNH P.56502, (c) from BMNH P.56475.



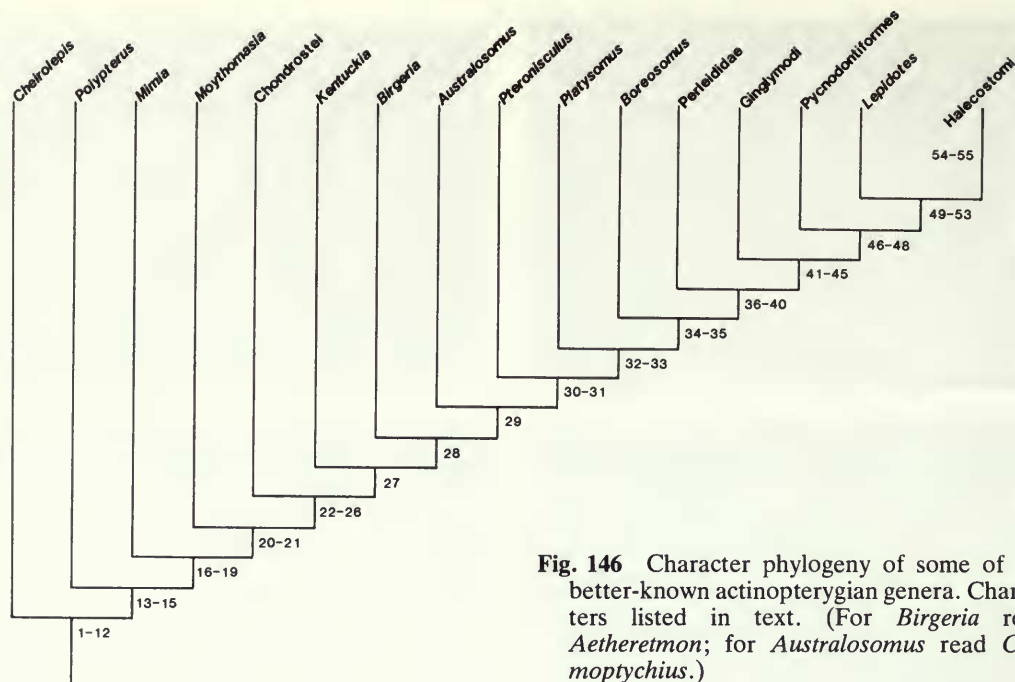


Fig. 146 Character phylogeny of some of the better-known actinopterygian genera. Characters listed in text. (For *Birgeria* read *Aetheretmon*; for *Australosomus* read *Cosmoptychius*.)

(*Carboveles*, *Platysomus*, *Pygopterus*, *Polyodon*, *Lepisosteus*, generalized teleosts etc.), or from anal, dorsal and lower caudal (*Cryphiolepis*, haplolepidids), or missing altogether (*Polypterus*, many teleosts). The basal fulcra are unpaired except above the tail in *Cheirolepis* where the first two scales are unpaired and the remaining 40–50 paired.

A single unpaired structure occurs in front of the median fins of *Osteolepis* and at least the dorsal fins of *Uranolophus*. However, only actinopterygians possess the long row of basal fulcra on the dorsal margin of the tail and these must be considered synapomorphous for actinopterygians (Patterson 1982).

3. Fringing fulcra

These are paired, leaf-like structures attached to the leading fin-rays which in fossils are difficult to distinguish from the dichotomously branched ends of the lepidotrichia. Fringing fulcra are unique to actinopterygians but their distribution is very spasmodic. They are found in *Mimia*, *Moythomasia*, *Pteronisculus*, *Perleidus*, *Ptycholepis*, redfieldiids, *Lepisosteus*, many fossil neopterygians and primitive teleosts (upper margin of tail in *Megalops* and *Tarpon*), but are absent in *Tegeolepis*, *Cheirolepis*, *Styracopterus*, *Amia*, *Polypterus*, chondrosteans, pycnodonts and most living teleosts.

In *Elonichthys* the fringing fulcra are delicate with up to two pairs per lepidotrichial segment in *E. robisoni*. In *Lepisosteus* and *Meidiichthys* (BMNH P.1607) the basal fulcra grade into fringing fulcra and in many fossil actinopterygians (parasemionotids, *Caturus*, *Semionotus*, *Dapedium*, *Ophiopsis*) the fringing fulcra are particularly stout and form a sturdy 'cutwater'.

Phylogenetic results

Interrelationships of actinopterygians

Although most recent authors have regarded the Cladistia as actinopterygians (Goodrich 1930, Daget 1950, Gardiner 1973, Rosen *et al.* 1981, Forey & Gardiner 1981), some authorities have considered them a separate group of osteichthyans (Jarvik 1942, 1980, Nelson 1969b). Patterson (1982), in a critical examination of the evidence, concluded that they are the sister-group of

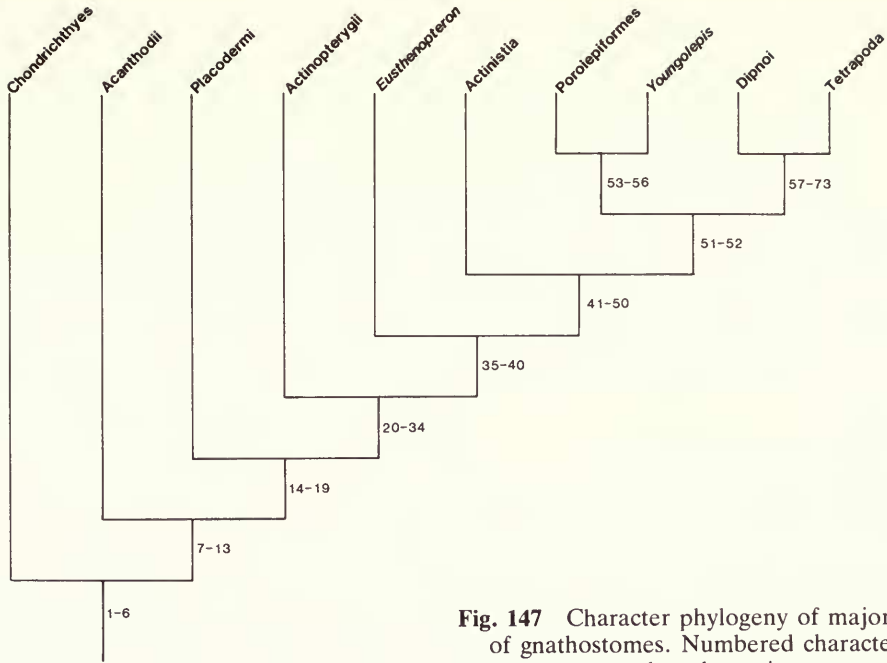


Fig. 147 Character phylogeny of major groups of gnathostomes. Numbered characters refer to synapomorphy scheme in text.

Actinopteri and this view is supported by the numerous synapomorphies listed by him. These include teeth with an apical cap of acrodin, the reduction of the jugal canal to a horizontal pit-line and the absence of a squamosal, presence of a valvula, otoliths formed of vaterite, gill-arch and jaw musculature, a protractor hyomandibularis muscle and pectoral propterygium.

Cladistia also share with Actinopteri buried layers of ganoine on the surface of dermal bones and ganoid scales with an anterodorsal process and peg-and-socket articulations. These characters are missing from living *Chondrosteus*; however, there is an anterodorsal process on the scales of *Chondrosteus* (BMNH P.41615) and I have also observed small pustules of ganoine on some of the head bones of *Chondrosteus*. Since *Chondrosteus* is the sister-group of the Acipenseridae (Patterson 1982: 253) the absence of these characters in Chondrostei must be rated as secondary.

Other features common to cladistians and generalized actinopterygians, but absent in Chondrostei, include a dentary with an enclosed sensory canal, a dermohyal, presupracleithrum, a shield-like rostral with an enclosed ethmoid commissure, a dilatator operculi muscle and a levator arcus palatini muscle inserting on the dorsolateral surface of the palate.

Finally, cladistians share with Actinopteri, including chondrosteans, a parasphenoid with an ascending process and a posterior stem. I have argued elsewhere (Gardiner 1973: 116, and above) that the parasphenoid has grown back independently on several occasions, and conclude that the posterior stem in cladistians is non-homologous with that of chondrosteans which in turn is non-homologous with that of other Actinopteri. I also regard the ascending processes as non-homologous in cladistians and actinopterans. In actinopterans the ascending process is developed in the spiracular groove, whereas that in cladistians is large and complicated with medial, lateral and ventral components and has a different phylogenetic history (Patterson 1982).

Within the Actinopteri the Chondrostei and Neopterygii are generally regarded as sister-groups (Nelson 1969b; Patterson 1973, 1982). Shared synapomorphies include a spiracular canal which opens into the fossa bridgei, an ascending process of the parasphenoid which reaches or enters the spiracular canal, a supramedullary hemopoietic organ (presumed to occupy the lateral cranial canal of fossil forms), three ossifications or cartilages in the hyoid

bar, a swimbladder and nasal rosette, a perforated pectoral propterygium embraced by marginal rays, a middle region to the endoskeletal pectoral girdle, and a dermopterotic.

In summary, if only Recent fishes are considered the most economical distribution of character states places Cladistia as the sister-group of Chondrostei plus Neopterygii.

The Neopterygii may further be divided into Ginglymodi and Halecostomi (Patterson 1973). Neopterygian synapomorphies include:

- symplectic developed as an outgrowth of the hyomandibular cartilage;
- quadratojugal which braces the quadrate;
- premaxilla with an internal process lining the nasal pit;
- reduction of body lobe of tail;
- symmetrical caudal fin in which the outer principal rays of the upper lobe approximately equal those of the lower lobe in length;
- dorsal and anal fin-rays equal in number to their endoskeletal supports;
- antorbitals;
- articular with a coronoid process;
- dermal basipterygoid process;
- hyomandibula with opercular process;
- palatoquadrate disconnected from dermal cheek bones posteriorly and dorsally;
- preopercular with narrow dorsal limb no longer in contact with the maxilla.

Primitively in actinopterygians the palatoquadrate is assumed to have been tied to the maxilla anteriorly, the preopercular dorsally and the quadratojugal posteriorly, thereby entirely enclosing the adductor mandibulae muscle in a tube of bone. Although the preopercular is missing in chondrosteans the adductor mandibulae muscle is still inserted on the outer surface of the palatoquadrate as in selachians. However, in neopterygians, where both dorsal and posterior contacts between the dermal cheek bones and the palatoquadrate have been lost, the adductor mandibulae is inserted on the neurocranium as well as the palatoquadrate. In cladistians, although contact is maintained between the palatoquadrate and preopercular posteriorly, the palatoquadrate turns inwards dorsally, not outwards as in acanthodians, selachians and chondrosteans, to lie in a nearly horizontal position with its edge fitting into a groove on the parasphenoid (a unique condition). The adductor mandibulae muscle is inserted on the preopercular, palatoquadrate, hyomandibula and neurocranium. I consider the loss of the dorsal connection between the palatoquadrate and preopercular and the concomitant insertion of the adductor muscle on the neurocranium to have occurred independently in cladistians and in neopterygians.

In halecostomes the anterior connection between the palatoquadrate and maxilla is also lost and the group is characterized by a mobile maxilla with a peg-like internal head. Other synapomorphies include:

- enlarged posterior myodome occupying at least half the distance between the pituitary fossa and the vagus foramen;
- pre-ethmoids;
- large post-temporal fossa without an endoskeletal roof;
- supramaxilla and interopercular;
- epibranchials with uncinate processes;
- intercalar with membranous outgrowths over the surface of the otic region;
- loss of the quadratojugal as an independent element;
- development of a post-temporal process.

A post-temporal process is also said to be present in *Polypterus* (Allis 1922: 206) and *Lepisosteus* (Jessen 1972: pl. 9, fig. 4), but these processes bear little resemblance to those in halecostomes and are therefore regarded as convergent.

Having outlined a phylogeny of Recent actinopterygians it is now possible to establish the approximate order of origin of specializations within the group.

The order Palaeonisciformes is generally considered to include the most primitive

actinopterygians (Kasantseva-Seleznevsk 1981) and *Mimia* and *Moythomasia* have both been assigned to that Order (Gardiner 1973). In the past most of the propositions of relationships of palaeoniscids have been couched in ancestor–descendent sequences (e.g. Gardiner 1963, 1967), but a cladistic examination (Patterson 1982) has revealed that the palaeoniscids constitute a paraphyletic group. It further showed that *Cheirolepis* is the sister-group of the Actinopterygii, *Mimia* is the sister-group of the Actinopteri + *Moythomasia*, but that the vast majority of the palaeoniscids are more closely related to the Neopterygii. It also revealed one major anomaly, the absence of a posterior myodome in *Lepisosteus*. A posterior myodome is present in all advanced palaeoniscids and in halecostomes (apart from a few teleosts where it is assumed to have been secondarily lost). However, from the congruence of other features, its absence in *Lepisosteus* is rated as secondary.

The advanced features are now listed in their approximate order of origin in a synapomorphy scheme which is summarized in Fig. 147 and in the classification.

A. *Cheirolepis* shares with other actinopterygians:

1. An anterodorsal angle or process to the scale
2. Ganoine
3. Dentary with enclosed mandibular sensory canal
4. Jugal canal not joined to infraorbital canal (except in *Polyodon*); instead it is reduced to a horizontal pit-line
5. Squamosal absent
6. Palatoquadrate joined to preopercular dorsally, and to quadratojugal posteriorly
7. Dermohyal covering head of hyomandibula only
8. Presupracleithrum
9. Pectoral propterygium
10. Otoliths formed of vaterite
11. A shield-like rostral with enclosed sensory canal commissure (except Chondrostei)
12. Basal fulcra on upper border of tail.

B. *Polypterus* has the foregoing characters (except 12) and shares with actinopterygians:

13. Acrodin caps on all teeth
14. Peg-and-socket articulations between scales
15. Postcleithrum.

C. *Mimia* has all the foregoing characters (except 13: some teeth without caps) and shares the following derived features with Recent actinopterygians:

16. Perforated propterygium
17. Bases of marginal rays embrace propterygium
18. A middle region to pectoral girdle
19. Lateral cranial canal.

D. *Moythomasia* has all the foregoing characters and shares the following derived characters with Recent actinopterygians:

20. An ascending process on the parasphenoid which lies in the spiracular groove
21. Supra-angular.

E. Chondrostei have the foregoing characters apart from 3, 4, 6, 7, 8, 11, 14, 15 and 19, and share with neopterygians:

22. A spiracular canal
23. An ascending process which reaches or enters spiracular canal
24. A fossa bridgei
25. A dermopterotic
26. Three ossifications or cartilages in the hyoid bar.

It is worth noting that Patterson (1982) has recorded acrodin caps on the teeth of large

Polyodon, a supra-angular in *Chondrosteus* and I have observed ganoine on the dermal bones of *Chondrosteus* and scales with an anterodorsal angle.

F. *Kentuckia* has the characters of A–E (except perhaps 24, but characters 8, 9, 10, 12, 15, 16, 17, 18, 21, 26 not known) and shares the following derived character with primitive neopterygians:

27. Myodome.

G. *Aetheretmon* has the foregoing characters apart from 8 and 15 (19 not known) and shares the following derived character with neopterygians:

28. Suborbitals.

H. *Cosmoptychius* has the foregoing characters apart from 8 and shares the following derived character with neopterygians:

29. Unpaired myodome.

I. *Pteronisculus* has the foregoing characters and shares the following derived characters with neopterygians:

30. Dermal basipterygoid process

31. 'Prismatic' ganoine.

The term 'prismatic ganoin' has been used by Ørvig (1967a, 1978) to describe the appearance, when viewed by polarized light, of the superposed generations of ganoine on the scales and dermal bones of many palaeoniscids and neopterygians. I have seen this type of ganoine on the scales of many palaeoniscids including *Elonichthys*, *Rhadinichthys*, *Gonatodus*, *Palaeoniscus*, *Acrolepis*, *Gyrolepis*, *Pygopterus*, *Centrolepis*, *Eurynotus* and *Pteronisculus*. It was not seen in *Cheirolepis*, *Polypterus*, *Mimia*, *Moythomasia*, *Stegotrachelus* or *Australosomus*.

Many Carboniferous palaeoniscids appear to be either interchangeable with or to fit somewhere near *Pteronisculus* in this cladogram; these include *Elonichthys*, *Rhadinichthys*, *Gonatodus* and *Kansasiella*. Unfortunately, the characters for which information is available do not provide sufficient evidence for establishing hypotheses of relationships.

J. *Platysomus* has the foregoing characters apart from 6, 7, 8, 11 and 28 (9, 10, 16, 17, 18, 19, 22, 24, 26, 29 not known), and shares the following derived characters with neopterygians:

32. Palatoquadrate detached from preopercular and maxilla dorsally and from the preopercular posteriorly

33. Preoperculum and hyomandibula almost vertical.

K. *Boreosomus* has all the foregoing characters with the exception of 6, 7, 8 and 15. It shares the following derived features with neopterygians:

34. Hyomandibula with an opercular process

35. Fringing fulcra on upper border of tail.

The tail of *Boreosomus* is abbreviate heterocercal, with the body axis not quite reaching the end of the dorsal lobe. On the upper border basal fulcra appear to grade into fringing fulcra, much as in *Lepisosteus*. An opercular process also occurs in *Polypterus* but this is rated as convergent.

Boreosomus marks the end of the grade group (stem-group) Palaeonisciformes, but between it and the neopterygians are several more advanced groups formerly designated 'subholosteans'. These include the Perleididae. Other 'subholosteans' such as the Redfieldiidae are either interchangeable with or fit somewhere near *Boreosomus* in the phylogeny.

L. Perleididae have all the foregoing characters apart from 6, 7 and 8 (29 not known) and share the following derived characters with neopterygians:

36. Elongate upper caudal fin-rays

37. Dorsal and anal fin-rays equal in number to their supports

38. Antorbitals and premaxillae

39. Premaxilla with an internal (nasal) process which lines the nasal pit

40. A dilatator fossa.

The dorsal and anal fin-rays also equal their supports in haplolepidids, *Bobasatrania*, *Luganoia* and *Platysiagum*.

M. Ginglymodi have all the foregoing characters except 6, 7, 27 and 29 and uniquely share with halecostomes:

41. A symplectic developed as an outgrowth of the hyomandibular cartilage and a quadratojugal which braces or supports the quadrate

42. Body lobe of tail reduced, symmetrical caudal fin in which outer principal rays of upper lobe approximately equal in length those of lower

43. Maxilla and preopercular lose contact with posterior margin of palatoquadrate

44. Articular with coronoid process

45. Preopercular with a narrow dorsal limb.

A coronoid process is developed in *Polypterus*, where it is composed solely of the prearticular. This is considered convergent with that of neopterygians which always incorporates lateral investing bones. The coronoid process of *Luganoia* is considered synapomorphic with that of neopterygians.

N. Pycnodontiformes have all the foregoing characters apart from 6, 7, 8, 11, 12, 15, 21, 28 and 35 (18, 19, 22, 24, 30, 31, 40 and 41 not known) and uniquely share with halecostomes:

46. A mobile maxilla with peg-like internal head

47. A large posterior myodome

48. Large post-temporal fossa.

In *Macromesodon* (Nursall 1966) the preopercular canal appears to have joined the infraorbital, much as in paddlefishes; this is assumed to be secondary. Although the jaw articulation is not known with certainty, there is a rod-like bone buttressing the quadrate in *Microdon* which has the appearance of a quadratojugal.

O. *Lepidotes* has the foregoing characters apart from 6, 7, 9 and 11 (16 not known) and uniquely shares with halecostomes:

49. A supramaxilla

50. An interopercular

51. Epibranchials with uncinat processes

52. A post-temporal with an internal process of halecostome type

53. Post-temporal fossa confluent with fossa bridgei.

Epibranchials with uncinat processes also occur in *Australosomus*.

P. Halecostomi have all of the foregoing characters except 6, 7 and 11, and in addition possess:

54. An intercalar with membranous outgrowths over the surface of the otic region

55. A quadratojugal which no longer remains as an independent element.

Classification

The broad phylogenetic results based on the synapomorphies cited in the text are summarized in the following outline classification, which follows the conventions of Patterson & Rosen (1977). '†' indicates an extinct group.

SUPERCLASS Gnathostomata

CLASS Chondrichthyes

SUBCLASS Selachii

SUBCLASS Holocephali

Plesion †Acanthodii

Plesion †Placodermi

CLASS Osteichthyes

- SUBCLASS Actinopterygii
 - INFRAClass Cladistia
 - INFRAClass Actinopteri
 - SUPERDIVISION Chondrostei
 - SUPERDIVISION Neopterygii
 - DIVISION Ginglymodi
 - DIVISION Halecostomi
 - SUBDIVISION Halecomorphi
 - SUBDIVISION Teleostei
- SUBCLASS Sarcopterygii
 - Plesion †*Eusthenopteron*
 - INFRAClass Actinistia
 - Plesion †Akinetia
 - ORDER †Porolepiformes
 - ORDER †Youngolepiformes
 - INFRAClass Choanata
 - SUPERDIVISION Dipnoi
 - SUPERDIVISION Tetrapoda

The more particular results concerning the interrelationships of actinopterygians are embodied in the classification below.

- SUBCLASS Actinopterygii
 - Plesion †*Cheirolepis*
 - INFRAClass Cladistia
 - INFRAClass Actinopteri
 - Plesion †*Mimia*
 - Plesion †*Moythomasia*
 - SUPERDIVISION Chondrostei
 - SUPERDIVISION Neopterygii
 - Plesion †*Kentuckia*
 - Plesion †*Aetheretmon*
 - Plesion †*Cosmoptychius*
 - Plesion †*Pteronisculus*
 - Plesion †*Platysomus*
 - Plesion †*Boreosomus*
 - Plesion †Perleididae
 - DIVISION Ginglymodi
 - Plesion †Pycnodontiformes
 - Plesion †*Lepidotes*
 - DIVISION Halecostomi

Relationships of actinopterygians

A character phylogeny of Recent and fossil gnathostomes has been presented by Rosen *et al.* (1981), in which they have suggested that the acanthodians are the most plesiomorphous gnathostomes, lungfishes are the sister-group of tetrapods and that rhipidistians are paraphyletic and form a stem-group series between actinopterygians and lungfishes. The phylogeny given below is essentially that of Rosen *et al.* except that the chondrichthyans are considered the most plesiomorphic gnathostomes and the placoderms the sister-group of osteichthyans. In addition the Porolepiformes + *Youngolepis* are considered the sister-group of the dipnoans and tetrapods (see Fig. 147).

A. Chondrichthyans share with other gnathostomes:

1. A lower jaw supported by a palatoquadrate and hyomandibula. Hyomandibula which contacts neurocranium

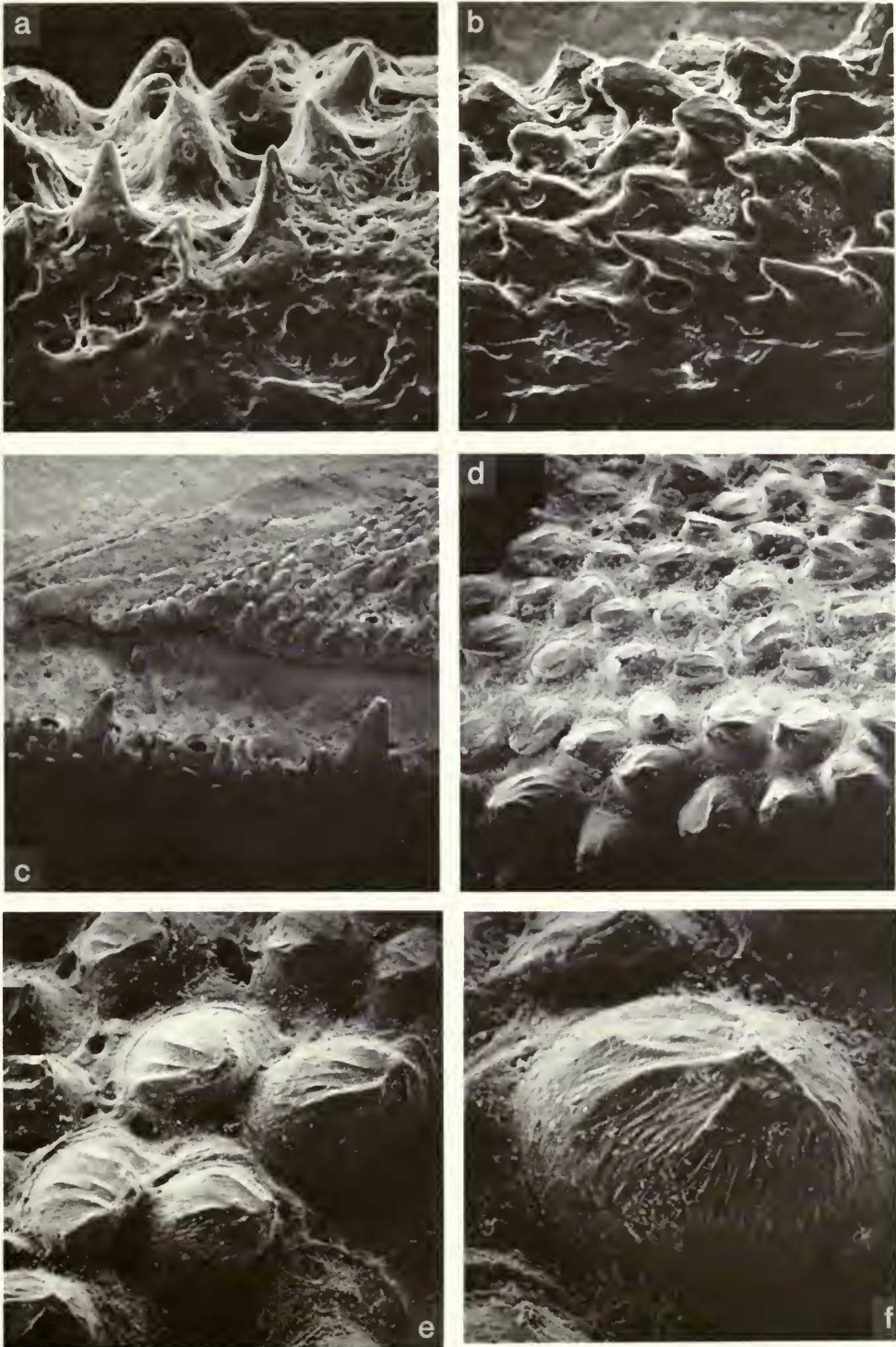


Plate 4 *Mimia toombsi* Gardiner & Bartram. (a), (b) coronoid teeth, $\times 150$. (c) anterior end of palatine with accompanying maxillary tooth row, $\times 30$. (d-f) palatine teeth, (d) $\times 100$, (e) $\times 200$, (f) $\times 500$. Scanning electron micrographs, all from BMNH P.53252.

2. A hyoid bar connecting the branchial apparatus with the hyomandibula
3. Anterior branchial arches consisting of hypobranchial which articulates with a basibranchial, ceratobranchial, epibranchial and pharyngobranchial elements
4. A cephalic lateral-line system that includes the following canal sections: supraorbital, infraorbital, supratemporal, mandibulo-preopercular, and jugal that joins the infraorbital and preopercular
5. Paired pectoral and pelvic appendages with internal supporting girdles and radials
6. Three semicircular canals.

B. Acanthodians also have the following derived features which they share with placoderms and osteichthyans:

7. Shoulder-girdle with ventral dermal plates and three perichondral ossifications
8. Operculogular series of dermal plates
9. Three ossifications in palatoquadrate
10. Two ossifications in Meckelian cartilage
11. Two ossifications in basibranchial cartilage
12. Dentigerous dermal plates on dorsal surface of Meckelian cartilage
13. Splenial bone.

The hypothesis that acanthodians and osteichthyans are sister-groups (Miles 1964, 1971a, 1973a) is supported by the presence of branchiostegal rays (8 above) and ventral dermal plates on the shoulder girdles (7 above), while the suggestion that they are the sister-group of chondrichthyans (Nelson 1968) is sustained by the posterior position of the gill skeleton and the posterior orientation of the pharyngobranchials. The double mandibular joint of *Acanthodes* is also said to be strikingly similar to that of amphistylid sharks (Miles 1973a: 71). The posterior position of the gill skeleton is a character shared only by selachians and acanthodians whereas the operculogular series and ventral plates of the shoulder girdle are found in acanthodians, placoderms and osteichthyans. The double jaw joint is seen in selachians, acanthodians and actinopterygians. However, since acanthodians uniquely share with placoderms and osteichthyans three ossifications in the palatoquadrate cartilage and two in the Meckelian cartilage, and have only a few ossification centres in the neurocranium, it seems more economical to interpret them as the sister-group of the osteichthyans + placoderms.

C. Placoderms have the foregoing characters apart from 13 (3, 11 not known) and share with osteichthyans:

14. Neurocranium protected by a series of large, interlocking dermal plates, some of which possess descending laminae of membrane bone
15. True dermal shoulder girdle with lateral plates to which scapulocoracoid is attached (viz. clavicle + cleithrum)
16. Supracoracoid foramen
17. Autopalatine articulates with postnasal wall
18. Dermal bone associated with the head of the hyomandibula (and completely covers the hyomandibula)
19. Parasphenoid with teeth, spiracular groove and foramen for buccohypophysial canal.

Evidence for the association of placoderms with osteichthyans has been presented by Forey (1980), who also cited the shared presence of endochondral bone. In my opinion (see p. 185) placoderms possess calcified cartilage, never endochondral bone. The competing hypothesis that placoderms and chondrichthyans are sister-groups (Stensiö 1963a, Miles & Young 1977) rests on two characters, the pelvic clasper and eye stalk.

Miles & Young (1977) have argued that pelvic and prepelvic claspers are most parsimoniously explained as a unique specialization of chondrichthyans plus placoderms. But only the ptyctodonts and holocephalans have both these structures. All other placoderms are devoid of claspers and selachians possess only pelvic claspers. Moreover the pelvic claspers in chondrichthyans consist of a varied number of articulated, cartilaginous segments supported by the distal end of the metapterygium, whereas that of ptyctodonts does not appear to have an

endoskeleton, projects ventrally from the root of the fin, and is covered by a laterally-toothed dermal plate. Distally the pelvic claspers are covered with dermal denticles in holocephalans, but the apex is usually naked in selachians except in the squaloids etc., where it is provided with one or more movable spines. The prepelvic claspers in pttyctodonts, like the pelvics, are supported by dermal bone only. They consist of a pair of flat plates which in *Ctenurella* bear spines. The corresponding structure in holocephalans is represented by a cartilaginous plate (grooved in *Callorhynchus*) covered with dermal denticles. Because of their different construction the pelvic and prepelvic claspers are accordingly rated as non-homologous in chondrichthyans and pttyctodonts. Eye stalks, or their scars, have been recorded in three genera of rhenanids, *Radotina* (Gross 1958: fig. 5A; Stensiö 1969: fig. 51), *Romundina* (Ørvig 1975: pl. 2, figs 1, 2) and *Brindabellaspis* (Young 1980: pl. 1, fig. 5; pl. 2, fig. 6), in arthrodires (*Buchanosteus* Young 1979) and in pttyctodonts, and in many selachians (*Oxynotus*, *Scyllium*, various myliobatids; Holmgren 1941). There are never any scars in xenacanth or hybodonts. The eye stalk chondrifies independently in selachians (Holmgren 1940: 109) and often leaves no trace of a scar in the wall of the orbit (e.g. *Chlamydoselachus*). The non-congruence with all other characters suggests that the presence of eye stalks is either a primitive gnathostome attribute or a chance similarity.

Finally Schaeffer (1975) considered placoderms to be the most primitive gnathostomes, based on the structure of the palatoquadrate. He suggested that their 'omega-shaped' palatoquadrate, in direct contact with the dermal cheek bones (viz. without a lateral cavity for the insertion of the adductor mandibulae muscles), was the primitive condition. Forey (1980), in contrast, considered it a synapomorphy of placoderms. However, the palatoquadrate of pttyctodonts and gemuendinids can by no stretch of the imagination be considered either 'omega-shaped' or in direct contact with the dermal cheek bones. Furthermore the adductor mandibulae muscle must have been inserted on the lateral face of the palatoquadrate in both *Ctenurella* (Miles & Young 1977: figs 24–28) and *Jagorina* (Stensiö 1959: figs 61–64), much as in generalized gnathostomes. An 'omega-shaped' palatoquadrate is therefore rated as a specialization of later placoderms, setting them apart from the more primitive pttyctodonts and gemuendinids.

D. Actinopterygians have all the foregoing characters (but the dermohyal only covers the head of the hyomandibula) and share with other osteichthyans:

20. Endochondral bone
21. Marginal teeth associated with premaxilla, maxilla and dentary (dental arcades), some of which undergo successional replacement
22. Premaxilla canal-bearing
23. Lepidotrichia in the fins
24. Suprapharyngobranchials on the first two gill arches
25. Radials of fins never extending to the fin margin (except in tetrapods)
26. Interhyal
27. Hypohyal
28. Gular plates
29. Subopercular
30. Basibranchial with consolidated toothplates
31. Anteriorly-directed pharyngobranchials
32. Gill arches 1 and 2 articulating on the same basibranchial
33. Separate branchial levator muscles, interarcual muscles and transversi ventrali muscles
34. Lung or swimbladder.

Rosen *et al.* (1981) listed a dermal sclerotic ring as a synapomorphy at this level. However, a sclerotic ring also occurs in placoderms (four plates), acanthodians (five plates) and cephalaspids (four plates); see p. 253.

E. *Eusthenopteron* has the foregoing characters apart from 18 (but 33, 34 not known) and shares the following derived features with actinistians, porolepiforms, dipnoans and tetrapods:

35. Exclusively metapterygial pectoral and pelvic fins, supported by a single basal

36. Teeth with enamel
37. Sclerotic ring of more than 12 segments
38. Enlarged otic or ascending process of palatoquadrate which articulates or fuses with neurocranium above the basitrabecular process
39. Submandibulars
40. Hyomandibular facet bilobed or double.

The palatoquadrate also articulates with the neurocranium in *Acanthodes*, but the articulation point is behind the postorbital process and is therefore rated as convergent, as is the fusion of the palatoquadrate in holocephalans. Rosen *et al.* (1981) also cite the presence of an anocleithrum as a synapomorphy at this level.

F. Actinistians have the characters of A, B, C, D and E apart from 3, 16, 18, 27 and 39, and share with Porolepiformes, dipnoans and tetrapods:

41. An unornamented anocleithrum
42. Clavicle large relative to cleithrum, and high pectoral appendage insertion
43. Pectoral and pelvic appendages with long muscular lobes and structurally similar endoskeletal supports
44. Preaxial side of pectoral fin endoskeleton rotated to postaxial position
45. A series of bones (the supraorbital-ectal series) lateral to the frontals and nasals which carry the supraorbital sensory canal
46. Presence of a rostral organ or labial cavity
47. A single, broad basibranchial
48. Last gill arch articulates with base of preceding arch
49. Reduction or loss of hypobranchials
50. An inferior vena cava and pulmonary vein.

G-1. Porolepiformes have the foregoing characters (24, 33, 34, 43, 44, 46, 50 not known) apart from 16, 18, 45 and 49, and share with dipnoans and tetrapods:

51. The immobilization of the intracranial joint
52. Cosmine pore-canal system in which the mesh canals are without a horizontal partition and the pore canals are enamel-lined.

That the intracranial joint was immobilized in porolepiforms is deduced from *Glyptolepis* (Jarvik 1972), in which the palate is fused to the postnasal wall anteriorly, into the 'fossa autopalatina' medially and to the basipterygoid process posteromedially, and where the articulation between the ascending process and the neurocranium is absent. This deduction is strengthened by the suggestion (below; see Jessen 1975: 213) that the Youngolepididae (*Youngolepis* and *Powichthys*) is the sister-group of the porolepiforms, since a suture often exists between the two shields of the skull roof in *Youngolepis* (Chang 1982) despite the fact that the underlying endocranium is ossified as a single piece. Moreover most of the specimens of *Youngolepis* that have been collected (Chang 1982: 7) are separate anterior cranial portions, much as in porolepids.

G-2. Youngolepididae (*Youngolepis* + *Powichthys*) also uniquely share with porolepiforms:

53. A 'fossa autopalatina' (Chang 1982: pl. 15A)
54. Foramen for the pituitary vein anterodorsal to the basipterygoid process (Chang 1982: 77)
55. Vomers widely separated by internasal pits and parasphenoid; internasal ridge
56. Much enlarged, downwardly pointing basipterygoid process.

Powichthys also shares with actinistians and dipnoans a series of bones lateral to the frontals which carry the supraorbital canal. Youngolepids may be distinguished from porolepids by the non-dendrodont form of their teeth.

A phylogeny of Recent gnathostomes rates the intracranial joint as a unique feature of *Latimeria*. Nevertheless there are several hypotheses about this structure, some of which have been generated to satisfy the assumption that rhipidistians rather than lungfishes are closer to tetrapods.

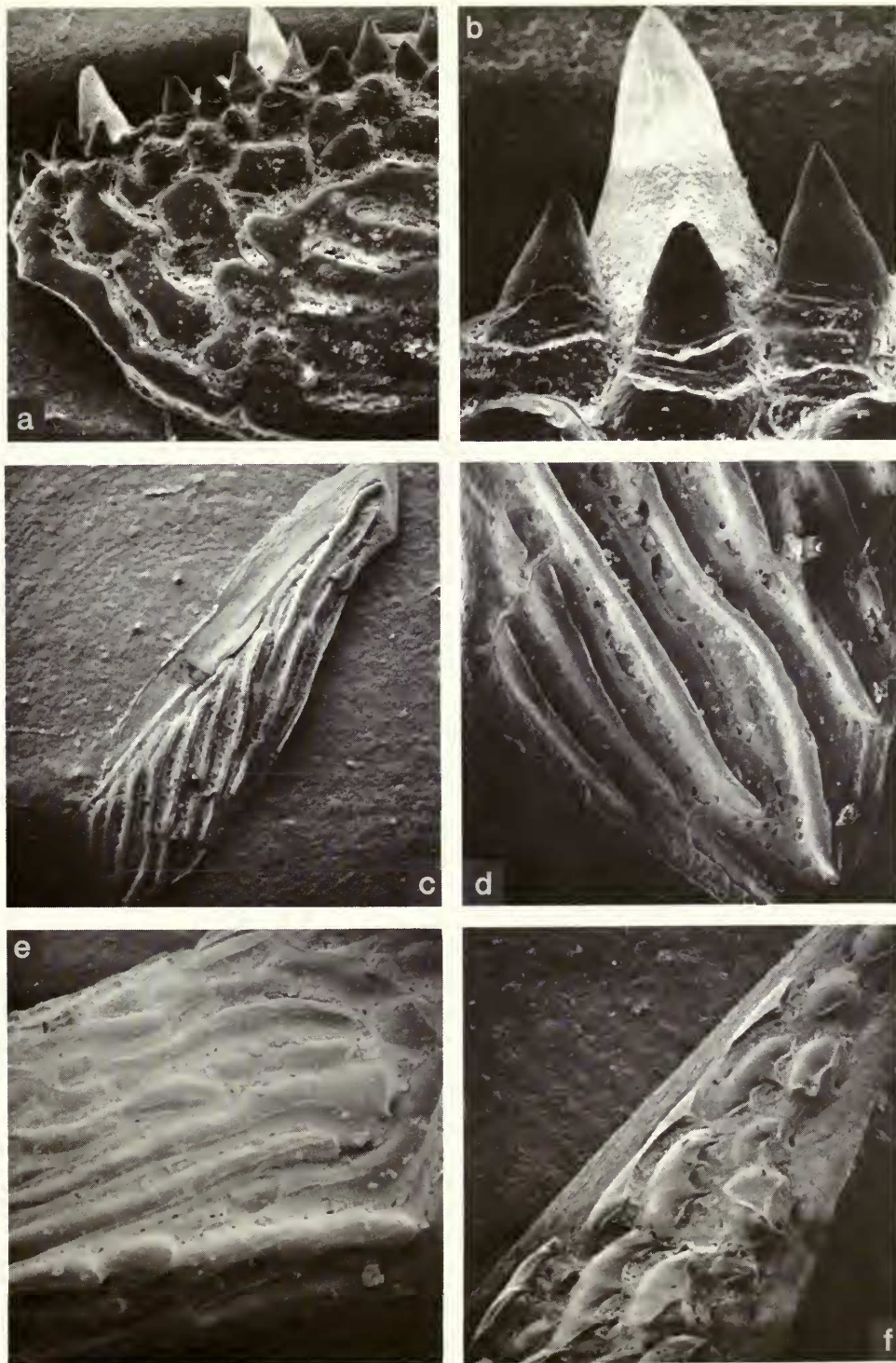


Plate 5 *Mimia toombsi* Gardiner & Bartram. (a) dentary tooth, $\times 30$. (b) dentary tooth, $\times 150$. (c) branchiostegal ray, $\times 20$. (d) posterior tip of branchiostegal ray, $\times 60$. (e) ornamentation of clavicle base, $\times 40$. (f) dorsal spine of clavicle, $\times 100$. Scanning electron micrographs, (a), (b) from BMNH P.53252, (c), (d) from BMNH P.56489, (e), (f) from BMNH P.56484.

The hypothesis that the intracranial joint is a primitive gnathostome character (Jarvik 1972) has been rejected because it leads to unacceptable phylogenetic conclusions (Miles 1977: 312; Forey 1980: 382). Another hypothesis, that it is a shared specialization of actinistians and choanates, separating this group from dipnoans (Miles 1977: 51), is also rejected, since no extant choanate possesses such a joint and its occurrence in fossil choanates is dubious (Rosen *et al.* 1981: 259; Gardiner 1983). The suggestion by Bjerring (1973) that the intracranial joint is not homologous in choanates and actinistians, which was arrived at by comparing the neurocrania of *Latimeria* and *Eusthenopteron* with the embryological condition in other gnathostomes, cannot be checked and is therefore regarded as speculation. The phylogeny outlined here interprets the intracranial joint as homologous in rhipidistians and actinistians, and therefore as a primitive feature of sarcopterygians. Further, it assumes that the joint has been lost once in porolepiforms (including youngolepidids) and choanates (dipnoans and tetrapods).

H. Dipnoans have all the foregoing characters except 2, 3, 18, 21, 22, 24, 26, 31 and 36, and those of G-2, and uniquely share with primitive tetrapods:

57. A choana
58. A labial cavity
59. Second metapterygial segment of paired appendages composed of paired, subequal elements that are functionally joined distally
60. Two primary joints in each paired appendage, between the endoskeletal girdle and the unpaired basal element, and between the basal element and the paired elements of the second segment. In the pectoral appendage, the preaxial member of paired elements with a ball-and-socket joint with the basal element and the postaxial member articulating on dorsal (postaxial) margin of basal element
61. Reduction in ratio of dermal fin-rays to supports in paired appendages
62. Muscles in paired fins segmented
63. Fusion of right and left pelvic girdles to form pubic and ischial processes. Presence of prepubic processes
64. Tetrapodous locomotion
65. Hyomandibula non-suspensory, reduced and associated with otic recess
66. Interhyal absent
67. Pharyngobranchials absent
68. Pterygoids joined in mid-line anteriorly, excluding parasphenoid from roof of mouth
69. Autopalatine absent
70. Elongation of snout region
71. Two pairs of dermal bones attached to the otico-occipital region of braincase posterior to parietals
72. Dentary with an oral pit-line
73. In soft anatomy, structure of lung, pulmonary circulation, two-chambered auricle, ventral aorta as a truncus, glottis and epiglottis, telolecithal jelly-coated bipolar egg, ciliation of the larva, pituitary structure including neurohypophysial hormone, lens proteins and bile salts, and gill-arch muscles.

Fusion of right and left pelvic girdles and prepubic processes also occur in many selachians, but this is considered convergent.

This phylogeny is summarized in the classification above (p. 399).

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Index

Numbers in *italics> are figure numbers.*

- abducens nerve 188, 192, 194–5,
197, 207, 224, 231, 248–9
canal 224, 249
- Acanthodes* 183–4, 189, 201, 203–4,
206, 208, 210–11, 213–15,
234, 240–1, 249, 253, 274,
282, 298–9, 301, 306, 332,
336, 342, 352, 356–60, 362–
3, 368, 380–1, 392, 402–3
bronni 120, 203
- acanthodians 183–5, 190, 203, 233–
5, 243, 253, 276, 295, 298–9,
306, 312–13, 325, 332–3,
336–8, 341–3, 352, 356–60,
362–3, 368, 374–5, 378, 380–
1, 392, 396, 400, 402–3
- Acanthodidae 336, 374
- Acanthodii 399
- Acanthostega* 312
- Acanthothoraci 336–7
- accessory hyomandibula 352, 356
opercular 344
toothplates 280
vomarine 53, 271, 273, 280,
310
- Acentrophorus* 267
- Acipenser* 183, 190, 198, 201, 203,
206–8, 211–12, 214, 227,
233–8, 240, 242–4, 246–9,
251, 267, 271, 276–7, 295,
297, 299, 301, 311, 324, 348–
9, 352–4, 359–60, 362–4,
368, 370–1, 374, 381–4
fluvescens 352
- Acipenseridae 395
- acrochordal 247
- acrodin cap 260, 264, 331, 395, 397
- Acrolepis* 398
- Acropholis* 305–6
- Acrorhabdus* 352, 370, 374
- Actinistia 177, 183, 400
- actinistians 203–7, 211–12, 214–15,
232–3, 238–41, 243, 246,
248, 253–4, 266, 270–1, 273–
4, 277–9, 295, 298–9, 301,
306–7, 311–14, 320, 324,
332–3, 339, 359–63, 365,
370, 374, 379, 392, 403–4,
406
- actinopteran 177, 181, 252, 277–8,
280, 339, 352–4, 360, 363,
380–1, 383, 388, 394, 397
- Actinopteri 395–7, 400
- actinopterygians 177, 183–5, 189,
191–2, 194, 196, 198–211,
214–16, 218, 228, 231, 233–
49, 251–2, 254, 257, 266–7,
270–1, 273–80, 293, 297,
299, 301, 305–7, 309–14,
316, 320–1, 324, 332–3, 339,
341–2, 344, 349, 352–3, 360,
362–6, 368, 372, 374, 378–9,
381–4, 386, 388, 392, 394,
396–7, 400, 402–3
- Actinopterygii 177, 183, 397, 400
- actinotrichia 386–7
- adductor hyomandibulae 245
mandibulae 243–6, 283, 396, 403
fossa 282–3, 286–7, 292, 307,
327, 331–3
opercularis 212–13, 244–5
- adotic process 232
- adsymphyseal plate 333
- Aetheretmon* 394, 398
- afferent hyoidean artery 346
- Agnatha 185, 228, 254
- Akinetia 400
- albulids 278, 339
- Alepocephalidae 233, 363
- alispheonid 299
(pterosphenoid) pedicel 230
- Alosa* 243
- Amblypterus* 251
- '*Ambipoda*' 204–5, 231, 275
- Ambystoma* 207, 210, 247
- Amia* 183, 192, 195, 198, 204, 206–
8, 210, 212, 214, 227, 230–1,
233–8, 242–9, 265, 267, 270,
275–7, 295, 297, 299, 305–7,
309–10, 313–14, 322, 324,
332–3, 339, 343–4, 346, 352,
357, 360, 362–3, 365–6, 368,
371, 378–9, 384, 386, 394
- amiids 183, 244, 267, 270, 277
- amioids 203, 206, 233, 240, 277
- amniotes 243, 322, 366, 380
- amphibians 207, 210, 243, 247, 297,
299, 301, 304, 311–14, 322,
332–3
- ampulla 212–13, 228
- ampullary chamber 211–12
anterior 227–8, 238
external 228
posterior 213, 216–17, 227–8
recess 228
- anal fin 364, 382, 384, 386, 392,
394, 396, 398–9
- anamestic bones 270
- anaspid 254
- anastomosis 270
- Anguilla* 342–3, 379
- anguillids 386
- angular 327, 331–3, 336
- anocleithrum 374, 378, 404
- anterior articulation 295, 297–8,
ascending process 271, 273, 277
basicapsular commissure 204
cerebral vein 226, 249–51
foramina 226
dorsolateral plate 376, 378
intraotic joint 205
lateral plate 376, 378
- median ventral plate 376
- dorsal fontanelle 216, 226
- myodome 254, 260, 264–6
bone 267
dorsal 254
ventral 254, 264–6
- nasal opening 259–60, 263–4
- otic process 301
- pit-line 317
- process 181, 299, 378
- semicircular canal 211, 228, 238,
241, 243
ventrolateral plate 376, 381
- anterodorsal scale process 395,
397–8
- anthracosaurs 243, 322, 333, 336
- Antiarcha 336–7
- antopercular 343
- antorbital 270, 396, 398
process 306
- antotic process 211, 215, 301, 306
- anurans 208, 299, 362, 380
- aorta 192, 406
- aortic canal 189, 191–2, 196, 201,
206–8, 273, 280
ligament 192, 201, 206
- Aphanerama* 311–12
- aphetohyoid hypothesis 357
- apodans 306, 360
- Arapaima* 278
- archaeomaenids 365
- Archegosaurus* 365
- Arctolepis* 253, 324
- arcualia 363–5
- Arthrodira 336, 403
- arthrodires 299, 306, 324, 332, 337,
341, 375–6, 381
- articular 325–6, 332–3, 336, 396,
399
fossa 299
- articular facet for palate 215,
260, 263–4
- ascending process of palate 239,
299, 301, 404
of parasphenoid 181, 211, 231,
234, 247, 271, 273, 275–9,
395–6
- aspidorhynchids 366
- '*Aspidorhynchus*' 183, 198, 214,
232–4, 237, 244–5, 247, 249,
252, 265, 277, 279, 295
- Atelaspis* (*Aceraspis*) *robusta* 254
- Attractosteus* 333
- auditory bulla 241
capsule 204, 235, 244, 248, 306,
363
diverticulum 244
nerve 195
region 241
- auricle 406
- Australosomus* 185, 189, 192, 195,

- 198, 203–5, 211, 231, 233–4, 236–8, 244–5, 251, 254, 264, 266, 271, 273, 275, 277–8, 280, 282–3, 295, 299, 307, 310, 332, 346, 362–5, 368, 384, 386, 398, 400
- autopalatine 282–3, 297–9, 305–8, 402, 406
- autostyly 246
- axial muscles 243
- skeleton 124, 363–8
- axonost 384, 386
- ball-and-socket joint 406
- basal connection 235
- fulcra 181–2, 392, 394, 397
- process 299, 301
- basibranchial 109–10, 120, 346, 348–9, 359–62, 402–4
- tooth plate 279
- basicapsular fenestra 203–4
- basidorsals 363
- basi-exoccipital 192, 194, 203, 208
- basihyal 360, 361
- basioccipital 184, 186, 188–9, 192, 194–6, 203–10, 214, 218, 234, 249, 275, 279–80
- basiotic lamina 235
- basipterygoid process 182, 213, 216, 222, 249, 271, 273, 276–7, 282–3, 286–7, 292, 299, 404
- dermal 276–7, 396, 398
- endoskeletal 276–7
- basisphenoid 22–24, 32, 188, 194, 204–5, 211, 213–16, 218, 222, 239, 241, 248–9, 271, 273, 275
- pedicel 214
- pillar 214, 218, 222–3, 230–1, 248–9
- basitrabecular 235
- process 301, 404
- basiventrals 363–4
- Batrachosuchus* 324
- Belonostomus* 366
- Benthosuchus sushkini* 76D
- Bergisch Gladbach 182
- bile salts 406
- birds 297, 360
- Birgeria* 182–4, 188, 198, 204, 206, 211–12, 231, 233, 237, 243–4, 251, 267, 275–8, 307, 310, 327, 360, 364, 368, 371, 384, 386, 398, 400
- Bobasatrania* 251, 275, 278, 295, 297, 312, 362, 386, 399
- bones X, Y₂, Y₁ 311–12, 322
- bony fishes 185
- vertebrates 185
- Boreaspis* 185
- Boreolepis* 306
- Boreosomus* 185, 189, 192, 198, 203–4, 211, 213, 228, 236–8, 241–4, 254, 264, 275–7, 282, 295, 299, 306–7, 312, 332, 339, 341, 343, 352, 363, 374, 382, 384, 386, 398, 400
- pivetaui* 188
- Bothriolepis* 253, 338, 341–2
- Brachyacanthus* 342, 374–5
- Brachydegma* 343
- Brachyosteus* 341
- brachythoracid 336–7
- branchial arches 108, 111–20, 234, 301, 344, 346, 349, 359–63
- levator muscles 231–3, 403
- nerve 346
- branchiostegal rays 97, 333, 338–9, 341–3, 348, 402; pl. 5c, d
- Brindabellaspis* 207–8, 210, 236, 240–1, 247, 266, 342, 381, 403
- stensioi* 185
- Broughia* 206
- bucco-hypophysial canal 216, 218, 271, 273, 278–80, 402
- duct 279
- Buchanosteus* 210–11, 240, 248, 279, 298–9, 403
- confertituberculatus* 185
- Cacops* 380
- calcified cartilage 185, 239, 332, 402
- Callopterus* 366
- Callorhynchus* 324, 357, 403
- canals for Sharpey fibres 387
- of Williamson 387
- Canning Basin 176
- Canobius* 371
- capsular ethmoid bones 267
- Carboniferous 278, 362, 365, 394
- Carboveles* 394
- carcharhinoid 207
- Carcharinus* 241, 297–8
- cartilage bones of palate 305–6
- catervariolids 365
- Catervariolus* 278
- caturids 183, 205, 216, 232–4, 236–8, 242–4, 247, 249, 265, 267, 270, 275–8, 295, 324, 366, 378
- Caturus* 198, 228, 233–4, 237–8, 242, 244, 247, 249, 265, 267, 279, 363–5, 392, 394
- chirotes* 277, 280
- furcatus* 277, 280
- caudal fin 385–6, 392, 394, 396, 398–9
- cavum sinus imparis 197, 201
- centra 208, 365–6
- central canal 324–5
- Centrolepis* 398
- Centrophorus* 235
- cephalaspids 185, 254, 403
- ceratobranchial 115, 120, 332, 346, 357, 359, 402
- fifth 349
- first 346
- fourth 349
- ligament 232
- second 348
- third 349
- Ceratodus* 271, 297
- ceratohyal 106, 120, 339, 342, 344, 346, 352, 357–60
- ligament 327
- ceratomandibular 301
- cerebellum 227
- Cetorhinus* 356, 368
- characinids 386
- Cheiracanthus* 253
- Cheirodus* 353
- Cheirolepis* 49, 182, 251, 267, 270–1, 273–9, 287, 292, 308, 311–12, 317, 324, 332–3, 339, 344, 352, 354, 357, 374, 378, 381, 386–8, 392, 394, 397–8, 400
- trailli* 77D
- chelonians 297, 306, 308, 360
- Chelydosaurus* 365
- Chimaera* 324, 368, 381
- chimaeroids 235, 342
- Chirodipterus* 182, 184–5, 201–2, 205–7, 210, 239, 248, 251, 271, 279, 297, 306, 311, 313, 324, 332–3, 341, 355, 360, 366
- Chlamydoselachus* 240–1, 267, 298–9, 301, 305, 313–14, 324, 333, 336, 403
- choana 270, 406
- Choanata 177, 301, 400
- choanates 247, 253, 297, 363, 406
- chondrichthyans 183–5, 211–12, 233–4, 236, 241, 243, 247–8, 266, 270, 276, 280, 298, 333, 342, 357, 359–60, 362–3, 368, 380–1, 383, 392, 400, 402–3
- chondrification 235
- chondrosteans 184, 190, 201, 203, 205–6, 211, 228, 237, 242, 244–6, 248, 266, 270, 275–8, 295, 297, 357–9, 370, 383, 386, 392, 394, 396
- Chondrostei 395–7, 400
- Chondrosteus* 206, 251, 271, 275–9, 297, 395, 398
- chordacentra 365–6
- circulus cephalicus 206
- circumorbital scutes 254
- Cladistia 395–6, 400
- cladistian 205, 339, 366, 368, 370, 394–5
- Cladodus* 207, 210, 235, 239–40, 298, 301
- Cladoselache* 207, 210, 298
- classification 399
- clavicle 126, 130–I, 134, 368–70, 375–6, 379, 381, 402, 404; pl. 5e, f
- cleithrum 126, 128–9, 131–2, 368–71, 374, 376, 378–9, 381, 386, 402, 404
- Climatiidae 374–5
- Climatius* 298, 341, 374–5
- cloacal scales 387

- Clupea* 307
 clupeid 243, 386
 clupeoids 206
Cobelodus 210, 241
Coccoderma 332
Coccolepis 275, 280
 coccosteids 324, 341
Cocosteus 253, 324, 352, 355
Coelacanthus 332
Commentrya 251, 343
 common carotid artery 276
Conchopoma 210, 279, 297, 361–2
 condyles of quadrate 282–3
 constrictor hyoideus dorsalis 212–13
 posterior part 212
 coracoid 126, 378–81
 anterior process 378–9, 381
 foramen 371, 378–81
 fossa 381
 portion 371, 374
Cornuboniscus 251, 374, 392
 coronoid 325, 327, 331–3, 336
 process 396, 399
 teeth pl. 4a, b
 cosmine pore-canal system 404
 cosmoid scale 392
Cosmoptychius 183–4, 189, 192,
 211–12, 234, 277, 280, 339,
 344, 394, 398
 cranial cavity 26, 201, 208, 213,
 215, 226–8, 231, 236, 242,
 246, 249, 251
 centrum 206
 fissure 203, 212, 231
 rib 191
 cranio-spinal process 190, 201
 cranium 234, 246, 251
Crassigyrinus 322
 Cretaceous 366
 crista occipitalis 198
 sellaris 247
 crossopterygians 321
Cryphiolepis 394
Cryptobranchus 210, 276, 306, 308,
 332
Ctenodus 322
Ctenurella 183, 210, 298, 301, 306,
 324, 332, 403
 gardineri 185
Cyclopterus 305
 cynodonts 380
 cyprinoids 206, 386
Cyprinus 378

Dapedium 192, 198–9, 205–6, 234,
 236–8, 242, 244–5, 247, 249,
 252, 265, 267, 276–7, 279,
 295, 392, 394
Dasybatus 241
Dendrerpeton 312
 dental arcades 403
 dentary 260, 263, 292, 326–7, 331–
 3, 336, 395–6, 403, 406;
 pl. 5a
 dentinal tubules 387–8
 dentine 336–7, 387–8, 392
 dermal basipterygoid process 273
 bones 185, 243
 cheek 77–8, 280, 287–92, 310–
 13
 lower jaw 332–8
 palatoquadrate 306–10
 shoulder girdle 126, 374
 skull roof 205, 217, 220, 244,
 316–24, 406
 snout 41, 48–9, 102, 254–71
 dermethmoid 270
 dermohyal 341–2, 344, 346, 349,
 352, 356, 395, 397, 403
 dermometapterygoid 283, 286–7,
 306–7, 309–10
 dermopalatine 283, 286–7, 292,
 295, 297–8, 306–10, 331
 dermopterotic 322, 396–7
 dermosphenotic 68–9, 181, 260,
 263, 291, 293, 310–12, 317
 descending laminae 324
 Devonian 176, 181–2, 185, 201,
 207–8, 210, 232, 239–41,
 243–4, 247–8, 253, 270, 277–
 9, 299, 333, 352, 360, 362,
 366
 stegotrachelid 181
 diapophysial outgrowths 368
 diazonal nerve 378, 380–1
Dicksonosteus 298, 306, 324, 337,
 352
 dicynodonts 380
 diencephalon 226
 dilator fossa 246, 399
 operculi 245–6, 352, 395
 Diplacanthidae 336, 374
Diplacanthus 325, 381
Diplocercids 204, 239, 266, 270–1,
 277, 299, 324, 332, 339
Diplomystus 277
Diplurus 324
 dipnoans 183, 185, 190–1, 201–8,
 210, 228, 232, 234, 238–41,
 243–5, 247–8, 251, 253, 257,
 266, 270–1, 273–6, 278–9,
 293, 295, 297, 299, 301, 304,
 306, 308, 311–14, 316, 320–
 1, 324, 331–3, 336–7, 339,
 341, 352, 355–6, 360–3, 366,
 368, 374, 379–80, 392, 400,
 403–4, 406
 Dipnoi 400
Dipnorhynchus 183, 251, 271, 273,
 279, 295, 306, 313, 320, 324,
 333
Dipterus 210, 253, 279, 313–14,
 321, 324, 332
 valenciennesi 279
Dirrhizodon 207
Discobatus 241
 dorsal anterior myodome 226, 244
 aorta 192, 206–7
 arterial system 276
 diverticulum 244
 fin 124, 363, 368, 384–6, 392,
 394, 396, 398–9
 hyoid constrictor 217, 228, 244–5
 ligament 368
 mandibular constrictor 245–6
 dorsomedial fin muscles 378
 dorsum sellae 214, 222, 247–9
Dorypterus 251
 dura mater 251

Eastmanosteus 336
Echidna 360
 ectopterygoid 283, 286–7, 292, 306–
 10, 313
Ectosteorhachis 206–8, 210–12,
 233–4, 238–40, 243, 245–6,
 248, 251, 266, 273, 278, 280,
 295, 354, 366
 edestid 392
Edops 312
 efferent arteries 234
 second 192
 pseudobranchial artery 271, 273–
 6, 278
Elonichthys 280, 306–7, 317, 324,
 353, 392, 394, 398
 aitkeni 306, 310
 binneyi 306, 310
 caudalis 310
 pectinatus 306
 robisoni 394
 semistriatus 310
 elopopocephalus 366
 Elopidae 233, 239, 363
Elops 232–3, 270, 278–80, 307, 309,
 324, 342, 346, 356, 363, 371,
 374, 381
Elpistostega 321
 enamel 404
 (acrodin) cap 260, 264
 endochondral ossification 182–5,
 195, 214, 218, 236, 403
 endolymphatic diverticulum 247
 ducts 202, 216, 228, 246–7
 fossa 202
 organ 246–7
 sac 247
 endoskeletal shoulder girdle 128–9,
 132, 371, 374, 378
Enneles 183, 244
 entopterygoid 246, 271, 273, 283,
 286–7, 292, 299, 307–10
Eogyrinus 312, 380
 attheyi 76C
 epaxial fin-rays 386
 lobe 386
 epibranchial 116–17, 234, 346, 349,
 352, 356–7, 359, 399, 402
 first 116, 233–4, 346, 362–3
 second 116, 348, 362
 third 117, 349
 epiglottis 406
 epihyal 349, 352
 epimandibular 301
 epineural 191, 366, 368
 processes 191
 epioccipitals 184, 198, 203, 212
 'epiotic' 212

- epiphysial crest 249
plexus 251
epipterygoid 299, 306
epurals 368, 386
Erriwacanthus 375
Errlichthys 275–7, 362
Eryops 380
esocids 386
ethmoid region 33–41, 254–71, 295, 297
ethmoidal bone 185
 commissure 259–60, 263, 267, 270, 395
ethmopalatine ligament 292
Etmopterus 235, 240, 301, 304–5
Euporosteus 266–7
Eurycormus 392
Eurynotus 398
euselachian 392
Eusthenodon 380, 312
Eusthenopteron 88G, 182–3, 201, 204–8, 210–12, 215, 232–5, 238–40, 242–6, 248, 251, 253, 258, 266–7, 270–1, 273–4, 276–80, 282–3, 295, 298–9, 301, 306–7, 311–12, 314, 321–2, 324, 332–3, 339, 343–4, 346, 349, 352, 354, 356, 360–3, 365, 368, 374, 400, 403, 406
 foordi 75C, 78A, 88F
Euthacanthus 325, 341, 375
excurrent opening 267
exoccipitals 184, 189, 197, 199, 203, 208–10
external rectus muscle 223–4, 231, 248–9
external semicircular canals 182, 203, 210, 212, 228, 243–4
extracleithrum 374
extracranial 218, 237–8
extralateral 341
extramural chamber 218, 236
extrascapular 84, 85–7, 125, 318, 324, 368
eye-stalk 402–3
facial nerve 207, 227, 230, 239, 251
 buccal branch 257, 260, 263, 267
 canal 218, 228, 230, 236–40, 248, 251
 external mandibular branch 327
 foramen 211, 214, 218, 224, 233
 ganglion 236–8
 hyoid branch 346, 349, 352
 hyomandibular trunk 218, 227–8, 236–40, 344, 349, 353–5
 internal mandibular branch 283, 292–3, 327, 332
 lateralis branch 227, 237–40
 mandibular branch 346, 349, 353–5
 otic branch 214, 216, 237, 244
 palatine trunk 227–8, 236
 recurrent lateralis branch 216, 218, 230
 fenestra endonarina communis 254, 257
 exochoanalysis 308
 exonarina anterior 257
 ovalis 204
first infraorbital bone (lachrymal) 260, 264
fissura oticalis ventralis 185
Fitzroy Crossing 181–2
Fitzroy trough 176
Fleurantia 271, 324
foramen magnum 189–91, 196–9, 201, 208–10
foramen olfactorium evehens 266
fossa autopalatina 404
 bridgei 216, 238, 241–3, 317, 395, 397, 399
 spiracularis 243
fragmentation hypothesis 183–4
Frasnian 176
fringing fulcra 181–2, 371, 374, 382, 384–5, 394, 398
frontals 80–3, 225, 259–60, 263, 267, 278, 291, 311, 316–8, 320–1, 404
Furo 267
 philpotae 365
fusion hypothesis 184, 312
Gadus 386
galeomorphs 235
Galeus 212
Galkinia 365
ganoine 228, 369–70, 387–8, 392, 395–6, 398
 ridges 259–60, 263–4, 374
 scales 395
 tubercles 260, 263–4
gasserian ganglion 230, 236–40, 249
Gasterosteus 235, 278, 305, 361
Gemuendina 253, 341
gemuendinids 403
geniculate ganglion 218, 225, 230, 236–40
geniohyoideus muscle 327
gill-arch muscles 406
gill-rakers 356
Ginglymodi 396, 399–400
glenoid fossa 325–6, 331, 371, 380–1
glossopharyngeal nerve 227
 foramen 203, 212–3, 218, 227, 232–3, 316
 supratemporal branch 212, 217, 242, 245
glottis 406
Glyptolepis 182, 204, 207, 211, 238–9, 243, 251, 266, 273, 275–80, 282–3, 295, 298–9, 301, 307, 311, 324, 332, 339, 357, 360, 365, 368, 404
 groenlandica 75D
Glyptopoma 307
Gnathorhiza 297
gnathostomes 184–5, 190, 202, 204–5, 207, 210, 234–6, 239–41, 244, 246–9, 253–4, 266, 276, 280, 298, 301, 313, 324–5, 333, 338–9, 349, 356–7, 359, 362, 364, 368, 380–1, 392, 400, 403, 406
Gogo 176, 181–2
 Formation 176, 181
 palaeoniscid 'A' 181
 palaeoniscid 'B' 181–2
 palaeoniscids 189, 204, 208, 211, 233, 237–8, 240–5, 248–9, 271, 350, 362; see *Mimia*, *Moithomasia*
Gonatodus 251, 307, 310, 344, 398
Goodradigbeeon 253
Griphognathus 182, 184–5, 191, 201–2, 205–6, 210, 228, 233, 239, 248, 251, 253, 258, 266–7, 271, 276, 279, 297, 306, 308, 311–14, 316, 324, 332, 341, 346, 352, 355, 360–3, 366, 368
 whitei 76A, 78D, 89C
gular plates 97, 100, 339, 341–2, 403
gymnotids 386
Gyracanthidae 374
Gyracanthides 375
Gyracanthus 375
Gyrolepis 398
Gyroptychius 312
haemal arches 122, 364–5
 canal 364
 spines 364, 386
Halecomorphi 400
halecomorphs 184, 211, 214, 228, 236, 242, 245–6, 297, 333, 359, 386
halecostomes 190, 195, 211, 236, 343, 352, 366, 368, 396–7, 399
Halecostomi 396, 399–400
haplolepidids 386, 394, 399
Haplolepis 339, 365–6, 368
Helodus 206
hemicentra 365
hemichordacentra 365
Hemicyclaspis 254
hemopoietic organ 242, 395
Hepsetus 235
Heptanchus 212, 241, 360
Heptanchias 299, 301, 304
Heterodontus 234, 240–1, 248, 298, 301, 360
Heterolepidotus 198, 232–4, 237–8, 242, 244–5, 247, 249, 265, 267, 277, 279, 280
Heterotis 235, 342
hexanchoids 235
Hexanchus 381
Hiodon 295
hiodontids 278
holocephalan 206–7, 234, 244, 246, 299, 324, 337–8, 352, 357, 360, 392, 402–4
Holocephali 399

- Holodipterus* 184-5, 210, 239, 270-1, 279, 297, 306, 332-3
Holonema 253, 298, 341-2
Holopetalichthys 324
Holoptychius 881, 211, 215, 249, 266, 270-1, 273, 278, 295, 311, 314, 324, 333, 339
 holosteans 211, 242, 244
Homalacanthus 253, 325, 342
 horizontal pit-line 287, 293, 313, 322, 395, 397
 semicircular canal 241
 hyal origin 235
 ray 352
 hybodont sharks 403
Hybodus 207, 210, 235, 239-41, 301
Hydrolagus 248
 hyoid arch 235, 344-6, 349-60
 bar 235, 395, 397, 402
 gill cover 341, 356
 operculum 342
 process 339
 ray cartilages 342, 352
 hyoideo-mandibularis nerve 313
 hyomandibula 104-5, 217, 235, 239, 241-2, 244-6, 283, 317, 338, 341-2, 344, 346, 349, 352-4, 356-7, 359, 396-8, 400, 402, 406
 hyomandibular adductor 231, 244-5
 cartilage 359
 facet 211-12, 216-17, 240-1, 244-6, 404
 gill-rakers 356-7
 protractor 395
 trunk 218, 227-8, 236-40
 hypaxial lobe 386
 hypobranchial 111-14, 332, 346, 349, 359-60, 362, 402, 404
 first 346, 349
 fourth 348
 second 348-9
 third 349
 hypohyal 107, 344, 346, 349, 357, 362, 403
 hypophyseal foramen 182
 recess 218, 222
 stalk 278
Hypsocormus 183, 267, 368, 378
 hypurals 364, 386

 ichthyodectids 277
Ichthyokentema 236, 277-8, 280, 333, 365
Ichthyophis 306, 332
Ichthyosaurus 308
Ichthyostega 76B, 78C, 89A, 271, 279, 311-12, 322
 ichthyostegids 206
 incurrent opening 267
 inferior oblique 254, 265-6
 rectus 249
 vena cava 403
 inferognathal 336-7
 infraorbital bones 291, 310, 313
 sensory canal 256-8, 260, 264, 266, 270, 287, 291-3, 310, 312-13, 322, 324-5, 399
 infrapharyngobranchial 118, 235, 346, 362-3
 articulation 234-5, 279
 first 218, 234-5, 346
 second 233-4, 348
 infraprelateral 338
 infravagal process 190
 interarcual muscles 403
 intercalar 184, 190-1, 203, 212, 231-3, 396, 399
 strut 233
 interclavicle 130, 134-5, 362, 368, 370, 374-6
 interdorsals 264, 365
 interhyal 283, 344, 346, 352, 357-9, 403, 406
 intermandibular muscle 327
 intermediating body 295, 297
 intermuscular septum 191, 198, 210
 first 191, 196-8, 201, 207
 second 196-8, 201, 207-8
 internal carotid artery 222, 230-1, 275-6, 283
 foramen 280
 rectus 214, 249
 internasals 271
 interolateral plate 376
 interopercular 343, 396, 399
 interorbital fenestra 265
 region 249
 septum 214, 249, 254
 interrelationships of actinopterygians 394
 intersegmental artery 363-4
 intertemporal 79, 82-3, 181, 216, 291, 310-12, 317-18, 322
 interventrals 365
 intervertebral arteries 192, 208
 intracranial 239-40
 joint 204-5, 207, 239, 241-2, 244, 279, 404, 406
 intramural 239-40
 chamber 247
 recess 236
Ionoscopus 366, 392
 Ischnacanthidae 336, 374
Ischnacanthus 324, 336
Isurus 301

Jagorina 240, 253, 295, 301, 306, 341-2, 352, 355, 368, 381, 403
Jamoytius 254
 jugal 70-3, 181, 287, 291-3, 310, 312-13
 canal 312-14, 316, 395, 397
 jugular canal 213, 216, 218, 224, 228, 230, 232, 235-41, 245, 251, 273, 277, 348
 groove 216, 232-3, 237
 vein 218, 235-6, 238-9, 241, 245, 249, 251
 Jurassic 244, 365; see Upper Jurassic
 Kansas palaeoniscid B 247
Kansasiella 182, 185, 188-9, 192, 195-6, 198-9, 204, 208, 211, 215-16, 228, 233, 236-8, 242, 244, 247, 249, 254, 264, 275, 277, 398
Kentuckia 185, 188-9, 192, 195-6, 198, 203-5, 211, 216, 228, 231, 236-8, 242, 244, 247, 249, 264, 275, 277, 280, 282, 299, 344, 398, 400
 deani 88A
 Kimberley Plateau 176
 Kokenhusen 182
Kujdanowiaspis 240, 248, 279

 labial cavity 406
Laccognathus 360
Lacerta 332
 lacertilians 297, 306, 360
 lachrymal 71-2, 74, 260, 264, 287, 291-3, 310, 313
Laemargus 324-5
Lamna 368
Lasanius 254
 labyrinth cavity 212, 227
 lateral aortae 192, 206-7, 234
 lateral commissure 211, 216, 218, 235-41, 246, 273, 277, 304-5
 lateral cranial canal 181-2, 211, 215-16, 227-8, 241-3, 316, 395-6
 dermethmoids 267, 270
 dorsal aortae 206, 279
 ethmoid 267, 280, 283, 292, 297-8
 line 318, 360, 368, 387, 402
 scales 387-8
 occipital 210
 postrostral 267
 lateralis branch 227, 237
 canal 218, 230, 238
 ganglion 218, 225-6, 230, 238, 249
 root 218
 laterohyal 352
Latimeria 204, 207, 209, 211-12, 215, 233, 238-40, 242-9, 251, 253, 266-7, 270-1, 273, 276, 279-80, 295, 298-9, 306, 311, 313, 324, 332-3, 339, 343, 346, 349, 352, 354, 356-7, 359-63, 365, 368, 392, 404, 406
Laugia 203, 212, 233, 239, 270, 332
Lawnia 251
Leiosteus 324
 lens proteins 406
Lepidosiren 210, 297, 343
Lepidotes 183, 192, 198, 205, 212-15, 234, 236-8, 242, 244-5, 249, 252, 267, 277, 279, 295, 307, 399-400
 latifrons 280
 lepidotrichia 364, 371, 374, 382, 384-6, 394, 403, 406
 lepisosteids 246

- lepisosteoid 206
Lepisosteus 183, 198, 204, 206–8, 210, 212–14, 216, 227–8, 233–8, 242–6, 248–9, 266–7, 270, 275–7, 295, 299, 305, 307, 312, 314, 322, 324, 327, 332–3, 339, 344, 346, 352, 357–8, 360, 363, 365–6, 368, 370–1, 378, 381, 384, 386, 392, 394, 396–8
 leptolepids 183, 191, 198, 203, 205–6, 208, 211–12, 214, 228, 232–4, 236–8, 240, 242–6, 249, 252, 270, 276–7, 280, 295, 333, 339
Leptolepis 237–8, 242, 247, 278, 324, 368, 378
Leuciscus 235
 levator arcus palatini 235, 245–6, 282–3, 395
 levator maxillae 245
 Lissamphibia 308, 336
 longitudinal intervertebral ligament 199, 201, 210
 loral plates 374–5
 lower jaw 90–6, 325–38, 359, 361
Loxomma 322
 loxommatids 271, 311, 322
Luganoia 312, 386, 398
Lunaspis 324, 341
 lungfishes 244
 lungs 406
Lupopsyrus 374
Lyrocephalus 312, 324

Macrepistius 183, 215, 232, 237–8, 247, 249, 265, 267, 277–8, 366
Macromesodon 252, 305, 307, 309, 312–13, 399
Macropetalichthys 240, 266
Macropoma 211–12, 233, 238–9, 267, 270, 298–9, 306–7, 313, 332–3
Macrosemius, macrosemiids 366
 mammals 185, 320
 mandibular arch 235
 bone 236
 commissure 235
 constrictor muscle 245
 gill-cover 339
 joint 402
 pit-line 327, 331
 plate 338
 ray 349
 sensory canal 326–7, 331, 333, 336–7, 397
 marginal rays 181, 397, 382
 masseter fossa 243
 maxilla 60, 65–7, 260, 263, 283, 286–7, 291–3, 307, 310, 312–13, 331, 396, 398–9, 403
 maxillary teeth pl. 4c
 Meckel's cartilage 301, 325, 332, 336, 338, 346, 402
 Meckelian bone 325–7, 331
 fenestrae 336
 ossification 332
 median basirostral 295
 dorsal plate 376, 378
 fins 145, 384–6
 intramural chamber 247
 lorical plate 374
 postparietal 312
 supraotic cavity 247
 medulla 242
Megalichthys 207, 270–1, 276, 280, 295, 299, 306, 352, 366, 368
Megalops 270, 394
Meidiichthys 394
Melanognathus 332
 membrane bone 203, 214, 231–2, 236, 247, 321, 362, 366, 368, 402
 mentomandibular 332, 336
 mentomeckelian 325, 327, 331–3, 336
Mesacanthus 253, 336, 341
 mesocoracoid 378
 arch 371, 378–80
 process 371
 mesodentine 336–7, 392
Mesonichthys 251, 307
Mesopoma 371, 392
Mesturus 252
 metapterygium 371, 374, 381–3, 402–3, 406
 metapterygoid 282–3, 286–7, 299, 305–6, 310
 metencephalic recess 249
Metoposaurus 312, 324
 metotic fissure 185, 204
Microdon 399
 middle cerebral vein 227, 230, 249–51
 canal 225
 pit-line 316
 region of pectoral girdle 378–80, 396–7
Millerosteus 324
Mimia 176–400 *passim*, esp. 181.
 toombsi 1–6, 11–26, 33–44, 50, 53–57, 60–63, 65, 68, 70–2, 75A, 79–82, 84–5, 90–3, 97, 101, 104, 107–8, 181, 185–8, 215, 254, 266, 271, 280, 316, 325, 338, 363, 368, 382, 384, 386, pls 1, 2a–c, 4–5
Monongahela 297
 monotremes 297, 299, 380
Mormyrus 378
Moythomasia 181–400 *passim*, esp. 181–2
 durgaringa 7–10, 27–32, 45–8, 58–9, 64, 66–7, 69, 73–4, 83, 87, 94–6, 99–100, 103, 105–6, 109–11, 114–15, 118D, F, 131–6, 138, 139B, 140, 141B, 142, 144, 182, 199, 228, 251, 260, 273, 292, 318, 331, 339, 349, 364, 374, 382, 385, 387, pls 2d–f, 3
 nitida 88B, 231, 251, 374, 382
 perforata 388
 musculus spiracularis 245
Mustelus 241, 299, 301, 324, 368
 myliobatids 403
Mylostoma 337
 myodome 195, 204–5, 207, 211, 214, 223, 237, 247–9, 266, 275–7, 396–9
 anterior 279–80
 myomere, first 208, 210, 280
 second 207–9

Namaichthys 307
 nasal 43, 46, 48–9, 254, 257, 259–60, 263–4, 267, 270–1, 293, 316–17, 404
 capsule 182, 254–5, 257–8, 266–7
 cavity 260, 266
 rosette 396
 nasobasal canals 254, 256–8, 266–7, 271
Necturus 357
Nematoptychius 251, 307, 310
 greenocki 306
Neoceratodus 183, 191, 206–8, 210, 234–5, 238–9, 243, 247, 251, 266, 271, 276, 297, 306, 312–14, 324, 333, 338, 343, 346, 352, 355, 357, 360–1, 365
Neonesthes 357
 neopterygians 190, 237, 244–6, 275, 332, 352, 357–60, 386, 394, 397, 399
 Neopterygii 395–7, 400
Neorhombolepis 366
 nervus lineae lateralis 199
Nesides 182–3, 207, 212, 232, 238–40, 243, 245, 248, 266, 273, 276, 279, 299, 301, 306, 314, 324, 352, 354, 356
 neural arches 121, 123, 198, 363, 365, 368, 386
 spines 363, 368
 neurocranium 7, 13, 50, 182–280, 291, 299, 306, 316, 318, 320–1, 378, 396, 402, 403, 406, pl. 1
 acanthodian 183–4
 actinistian 184
 chondrichthyan 183
 leptolepid 182–3, 203
 pachycormid 183–4
 pholidophorid 182, 185
 placoderm 183
 rhipidistian 184
 shark 183
 teleost 183–4
 tetrapod 184
 neurohypophysial hormone 406
 neurokinesis 184, 205
 neuromasts 225, 244, 293
Nostolepis 336, 392
 nostrils 270–1
 notidanids 304
 notochord 182, 196, 207–8, 363

- notochordal canal 189, 191, 195–6,
 201, 207
 plate 182
 sheath 365
 notopterid 206
Notorhynchus 368
- occipital arch 185, 189, 203, 206,
 210
 arterial supply 197
 artery 192, 196–8, 201, 207–8,
 210
 condyle 191, 210, 275
 fissure 185, 188–9, 191, 199, 201–
 5, 215, 217, 228, 245, 316,
 318
 myomeres 208–10
 nerve canal 198
 first 198, 208
 foramen 192, 196–7, 201, 208–
 10
 second 208
 third 191
 ossification 2–4, 184, 215, 234,
 280
 process 190
 region 4–6, 8–10, 12, 14–15, 185,
 188–9, 199, 203, 207–8, 279–
 80, 318, 349
 discussion 201–10
 segment 208
 occiput 184, 190, 197–8, 201, 206–8,
 210, 234, 280
 segmental structure 208–10
 oculomotor foramen 214, 218, 227,
 238
 nerve 248
 olfactory nerves 226, 254, 266
 canal 226, 254, 257, 260, 265–6
 organ 267
 oligopleurids 366
 onion-skin growth 387, 392
 onychodont 253–4, 287, 307, 311–
 13, 324, 333, 339
Onychodus 311–12
 opercular 99, 217, 244, 338–9, 342–4
 adductor 231
 bones 338, 342–4
 cartilages 338, 341, 342–3
 process 352–4, 398
 rays 342
 operculogular series 338–9, 341,
 402
Ophiopsis 366, 394
 ophthalmic artery 222, 230
 canal 251
 foramen 223
 opisthotic 186, 203, 211–13, 231–3,
 240, 245
 optic fenestra 214, 225, 227
 foramen 214, 249
 lobe 226–7, 249
 nerves 226, 228, 248–9
 oral sensory canal 331, 333, 406
 orbit 20, 30–1, 215, 218, 224, 226,
 230, 238, 249, 254, 260, 266,
 298–9, 313
 orbital artery 218, 228, 234, 236,
 238–40, 276
 cartilage 247, 301
 foramina 218
 groove 218, 234
 region 213, 215
 surface 20, 218
 orbitonasal artery 181, 189, 218,
 222, 266
 foramen 218
 canals 255, 265
 orbitosphenoid 214
 orbitotemporal region 14–17, 19–
 22, 27–31, 33, 210, 216, 231,
 247–54, 277, 306
Orectolobus 241
 orobranchial chamber 235
'Orodus' 392
Osmerus 295
Ospia 203, 228, 237–8, 242–3, 306–
 7, 332
 ossification centres 183–4, 210
 osteichthyans 177–403 *passim*
 Osteichthyes 399
 osteodentine 336
 osteoglossoids 277–8, 357, 360, 366,
 386
Osteoglossum 232
 osteolepids 254, 270–1, 277–8, 280,
 295, 299, 307, 310–12, 314,
 321, 324, 332
 Osteolepiformes 177, 288
 osteolepiforms 270, 320–1, 324,
 333, 339, 343, 362, 370, 374,
 379–80, 392
Osteorhachis 233, 247, 267
 osteostracans 336
 otic bones 232
 capsule 185, 195, 203–4, 212–13,
 235, 246
 nerve 214, 216, 237
 canal 237–40, 242
 foramina 218, 230
 process 246, 298–306
 of palatoquadrate 244
 recess 406
 region 1, 4–6, 11–12, 14–15, 27–
 8, 185, 191, 203, 210–18,
 227–8, 346, 348, 396
 shelf 235, 241
 otico-occipital 279
 otico-sphenoid fissure 181, 210,
 216, 218, 231, 241
 otolith 227, 395, 396
 chamber 211
Oxynotus 235–6, 239–40, 301, 403
- pachycormids 183–4, 203, 205–6,
 214–16, 233–4, 236–7, 240,
 244, 267, 270, 277, 280, 295,
 324, 339, 362, 365, 386
Pachycormus 183, 189, 192, 215,
 234, 237–8, 244–5, 249, 252,
 265, 267, 270, 275, 333, 374,
 378
- Pachyosteina* 341
Pachyosteus 341
Palaeacanthaspis, *palaeacanthaspids*
 381
Palaeoherpeton 312–14
Palaeomyxus 337
 palaeoniscids 177, 183–5, 188–90,
 192, 195, 198, 201, 203–7,
 211, 213–16, 226–8, 230–1,
 234, 236–40, 242–3, 245–6,
 248, 251, 260, 264–5, 267,
 270, 273, 275–8, 287, 292,
 306–7, 309–10, 322, 327,
 332, 339, 346, 352–3, 374,
 383–4, 386, 392, 397–8
 Palaeonisciformes 177, 396, 398
 palaeoniscoid 181
Palaeoniscus 371, 378, 381, 386,
 398
 Palaeozoic selachians 203
 palate 75–6, 331, 404
 palatine artery 222
 canal 222
 fenestra 218, 230, 237
 nerve 218, 224, 227–8, 236–8,
 240, 258
 ossification 298, 307–8
 process 298
 vein 222
 palatobasal articulation 298–301
 palatoquadrate 53–6, 58–60, 206,
 235, 245–6, 280–7, 293–310,
 336, 346, 396–8, 400, 402–4
 basal process 295
 cartilage 254, 282
 commisure 293–5
 ossifications 305–10
 otic process 244
 pterygoid process 297
 symphysis 295
Palaeoherpeton 299, 306, 311
Palaeosephurus 275–6
Panderichthys 271, 313, 321–2, 332
 parabasal canal 222, 230, 237–8,
 275–6
 parachordals 188–9, 204, 207
Paramblypterus 205, 251, 386
 parampullary process 199, 212,
 217–18, 231–3
Paraplesiobatis 313
 parapophyses 366
 parasemionotids 183, 198–9, 203–6,
 210–11, 231, 234, 236–8,
 240, 242–6, 249, 265, 267,
 270, 275–8, 280, 295, 332,
 392, 394
Parasemionotus 192
 parasphenoid 7, 13, 50–2, 181, 205–
 6, 210, 216, 218, 222, 231–2,
 234, 260, 271–80, 283, 286,
 299, 362–3, 395–6, 402, 404,
 406
 teeth 278–9, 402
 parasymphysial plate 333
Pareiasaurus 380
Parexus 374–5

- parietals 80–3, 311–12, 316–18, 320–2, 324
- paroccipital process 212
- parotic crista 243
- toothplates 51, 273, 280
- pars ganglionaris 236
- pars jugularis 236
- pectoral fin 137, 369, 371, 374, 381–3, 387, 404
- spine 380
- girdle 128–9, 132, 368, 274–381, 402
- propterygium 181, 371, 381, 395–7
- peg-and-socket articulation 392, 395, 397
- Pelobates* 324
- pelvic claspers 402–3
- fin 382–3, 387, 404
- girdle 138, 382–4, 402, 406
- perichondral ossification 182–5, 188–9, 192, 195–6, 199, 201, 203, 210–11, 213–16, 226, 228, 234, 241–2, 249, 251, 253–4, 266–7, 298, 306, 316, 321, 325, 327, 332, 344, 357, 359, 363, 371
- perichordal commissure 240, 360
- tissue 191
- Perleididae 398, 400
- perleids 183, 237, 267, 270, 386
- Perleides* 189, 203–5, 211–12, 214, 228, 231, 236–8, 242–6, 267, 275–80, 343, 374, 394
- cf. *stoschiensis* 183, 203
- Permian 392
- Petalichthyida 336
- petalichthyids 341
- Phaneroosteon* 368, 392
- pharyngobranchial 233–4, 301, 359, 362–3, 402–3, 406
- pharyngoepihyal 349
- pharyngohyal 241, 349, 352
- pharyngomandibular 301
- Phylactenaspis* 253
- phylacteniid 337, 341, 356
- pholidophorids 182–3, 191–2, 195, 198, 203, 205–6, 208, 210, 214–16, 228, 232–4, 236–8, 240, 242–7, 249, 252, 265, 267, 270, 275–7, 280, 283, 339, 357, 362–3, 365, 386
- Pholidophorus* 189–90, 197–9, 203, 211–12, 214–16, 227–8, 230, 234, 237–8, 242–3, 267, 305, 364, 378
- bechei* 183, 188, 201, 203, 214–16, 277–8, 280
- germanicus* 198, 332
- higginsii* 333
- macrocephalus* 252
- pholidopleurids 183, 189, 192, 203, 205, 233, 237, 264, 275, 365–6, 386
- phyllolepis 324
- phylogenetic results 394
- pila antotica 218, 236, 239, 247–8
- pineal foramen 182, 216, 226, 316–17, 320
- pituitary 249, 406
- canal 222
- fossa 218, 227, 231, 396, 404
- vein 188, 222, 249
- Pinkus' organ 244
- pinnal plates 375
- pit-line 260, 313, 322, 324, 327, 331, 339, 341
- Placodermi 399
- placoderms 183, 185, 190, 207–8, 210–11, 228, 233–6, 240–1, 243, 247–8, 253, 266, 270–1, 275–6, 278–9, 295, 298–9, 301, 306, 313, 321, 324–5, 332, 336–7, 341–2, 352, 355, 368, 374–6, 378, 381, 392, 400, 402–3
- Placodus* 308
- placoid 392
- Platysium* 343, 386, 399
- Platysomus* 277, 394, 398, 400
- Plegmolepis* 346
- polar cartilages 188, 241, 247–8, 299
- Polyodon* 183, 185, 190, 198, 206, 212, 233–4, 236–7, 239–40, 242–4, 270–1, 277, 295, 297–8, 312–13, 324, 333, 339, 353, 358, 360, 363–4, 382–4, 394, 397–9
- Polypterus* 88D, 183–4, 189–90, 192, 194–6, 198, 203–8, 210–12, 214, 216, 227, 231–4, 236–8, 240, 242–9, 251, 260, 266–7, 270, 275–80, 283, 292–3, 295, 297–9, 305–6, 309–11, 313–14, 324, 327, 331–3, 336, 339, 342–3, 346, 349, 352–4, 356–7, 360, 362–4, 366, 368, 370–1, 374, 379–82, 384, 386–8, 392, 394, 396–9
- bichir* 75B, 77C, 295
- Poracanthus* 392
- pore canal 392
- porolepids 254, 270–1, 273–8, 280, 295, 298–9, 301, 306–7, 311–14, 324, 332, 368, 374, 404, 406
- Porolepiformes 177, 400, 404
- porolepiforms 278, 320, 324, 333, 339, 360–2, 370, 403–4
- Porolepis* 238, 240, 258, 266, 273, 278, 280, 283, 295, 299, 324, 339, 341
- brevis* 78B, 88E
- postbranchial lamina 376
- postcleithrum 127, 133, 370, 374, 397
- posterior ascending process 273, 277
- basicapsular commissure 204
- cerebral vein 197, 199, 201, 215, 217
- dorsal fontanelle 185–6, 189, 199, 201–3, 206, 215–16, 247, 318
- myodome 247–9, 266, 396–9
- nasal tube 257
- nostril 260, 263–4
- pit-line 317, 324
- semicircular canals 182, 212, 216, 227–8, 231, 241–3, 246
- stem of parasphenoid 273, 395
- post-ethmoid portion of neurocranium 25–6
- postfrontal 311
- postnasal wall 254, 257, 260, 263–4, 266–7, 298, 402, 404
- postorbital 310–12, 322
- process 211, 215–16, 224, 226, 235, 238, 240, 242–3, 245–6, 291, 301, 318
- postotical process 212
- postpalatine process 235
- postparietals 320–2, 324
- postrostral 267, 271
- postspiracular 339, 343
- postsplenial 336
- postsuborbital 306
- post-temporal 86–7, 125, 190, 318, 368, 376, 396, 399
- fossa 212, 239, 242–3, 246, 399
- process 396
- Powichthys* 311, 324, 404
- prearticular 327, 331–3, 399
- pre-ethmoids 267, 396
- pre-epiotic pocket 243
- prefacial commissure 218, 236–7
- floor 237
- prelateral 338
- premaxilla 44, 47–9, 254, 256–60, 263–4, 270, 292–3, 396, 398–9, 403
- preopercular 59–63, 283, 287, 291–3, 312–13, 338, 342, 396–9
- sensory canal 287, 293, 312–13, 399
- preoperculo-jugal canal 312
- prepalatine floor 230, 237
- strut 237
- prepubic process 406
- prespiracular cartilage 301, 304–5
- groove 276, 278
- presplenial 333
- presupracleithrum 339, 395, 397
- prismatic calcifications 184
- ganoine 398
- profundus canal 218, 230, 239–40, 266
- foramen 218, 238, 240
- nerve 227, 248, 255, 258, 266–7
- root 238
- pristiophorids 239
- Pristiophorus* 241
- Pristis* 241
- Pristiurus* 247, 381
- processus lingualis 360
- Procolophon* 380
- procoracoid 380

- Proleptolepis* 333
 prootic 184, 186, 188–9, 192, 195, 203–5, 207, 211, 214, 216, 218, 232–4, 236, 240–2, 246–9, 251, 273, 363
 bridge 182, 188, 194–5, 207, 239, 247–9
 knob 232
 process 235
 propterygial canal 381
 propterygium 136, 371, 374, 382
Protogonacanthus 253
Protopterus 210, 297, 314, 316, 324, 368
Protosphyraena 183
 protractor hyomandibularis 245–6, 352
Pseudocarcharias 301
 pseudopetalichthyids 336, 341, 381
Pseudopetalichthys 341, 381
 pseudoprismatic 388
Pteronisculus 182, 185, 188–9, 192, 195–9, 201, 203, 205, 207, 211–12, 214–6, 227–8, 233–4, 236–8, 242, 244, 249, 251, 254, 264, 273, 275–80, 282–3, 286–7, 293, 295, 299, 305–7, 310, 314, 317, 326–7, 331–2, 338–9, 343, 346, 348, 357, 360, 362–4, 368, 370–1, 374, 381, 384, 386, 394, 398, 400
cicatosus 236
macropterus 185, 189, 204–5
magnus 88C, 183, 247
stensioides 204
 pterospheonoid 211, 213–15, 247, 249
 pedicel 230, 238, 247, 249
 pterotic 203, 212–13, 240
 pterygoid 283, 297, 307, 310, 406
Ptomacanthus 295, 298, 375
 Ptyctodontida 336
 ptyctodonts 185, 299, 306, 337, 368, 375–6, 381, 402–3
Ptyctodus 337
 ptycholepid 267, 270
Ptycholepis 394
 pulmonary vein 403, 406
 Pycnodontiformes 399–400
 pycnodonts 216, 275, 278, 295, 297, 307, 309, 386
Pygopterus 283, 343, 346, 365, 374, 384, 386, 394, 398
 quadrate 57, 282–3, 286–7, 305–7, 325, 359, 396, 399
 quadratojugal 57, 63–4, 283, 287, 291–3, 313–14, 396–7, 399
 pit-line 291, 293, 314
 radial plate 139, 384–6
 radials 371, 381–4, 386, 403
Radotina 403
Raja 235, 241, 301
 ramus lateralis accessorius foramen 218, 225
 rays 235, 241, 301, 304, 352
 recess for telencephalon 226, 249
 recti muscles 214, 223, 248–9
 Redfieldiidae 398
 redfieldiids 267, 394
Redfieldius 343
 relationships of actinopterygians 400
 'reptiles' 299, 308, 311
 restoration of fish 145
 skull 101–3
 retina 254
 retroarticular 327, 332
Rhabdoderma 211–12, 215, 239–40, 270–1, 298–9, 306, 313–14, 324, 332–3, 339, 362, 374, 379
elegans 77A
Rhadinichthys 371, 398
Rhamphodopsis 337
 rhenanids 253, 336, 341, 381, 403
Rhina 368
 rhinobatoids 239
Rhinobatus 240–1
Rhinodipterus 253, 322, 325, 341
 rhipidistian 177, 201, 203–8, 212, 215, 233–4, 238–41, 243, 246–8, 251, 253, 266, 270, 273, 277–80, 299, 311, 324, 339, 366, 368, 392, 400, 404, 406
Rhizodopsis 210–11, 239, 243, 245–6, 251, 266, 366
Rhynchodipterus 366
Rhynchodus 381
 ribs 363–4, 366–8
 dorsal 366
 pleural 366, 368
 ventral 366, 368
 ridge scales 386
Romundina 324, 337, 376, 381, 403
 rostral 42, 45, 48–9, 254, 256, 258–60, 263–4, 267, 270, 293, 317, 395, 397
 organ 404
 rostro-palatine articulation 297–8
 rostro-premaxillo-antorbital 270
Sabrinacanthus 375, 381
 saccopharyngoids 343
 saccular cavity 207
 recess 217, 225, 227
 sacculus 196
 saccus vasculosus 222
Sagenodus 297, 313
Salamandra 308
Salmo 235, 248, 297, 299, 305–7, 352, 361, 368, 371
 salmonoids 206, 386
 sarcopterygian 177, 271, 307, 342, 362, 374, 378, 392, 406
 Sarcopterygii 183, 400
 saurichthyids 276, 295, 386
Saurichthys 190, 198–9, 205–6, 236–8, 243, 254, 265, 271, 275–9, 306
Saurorhynchus 276
 scales 140–4, 182, 370, 386–8, 392, 398, pls 2, 3
 structure 143–4, 388
Scaphirhynchus 295, 301, 370, 382–4
 scapula 378–80
 scapular foramen 371, 378, 380
 anterior 378, 380
 portion 371
 process 381
 scapulocoracoid 378–81, 402
Scaumenacia 89B, 271, 297, 313, 322, 324–5, 341
 sclerotic bones 228, 251–4
 ring 228, 231, 251, 403–4
Scomber 198, 236, 374
 scorpaeonids 236
Scyliorhinus 301
Scyllium 210, 247, 301, 342, 402
Scymnodon 235, 239, 240
Scymnorhinus 240
 second segment 207
Sedowichthys 337
 selachians 183, 203–4, 206–7, 210, 214, 234–6, 238–41, 244–9, 251, 295, 298–9, 301, 304, 312–14, 324, 342, 349, 352, 355–6, 396, 402–3, 406
 Selachii 399
 semicircular canals 402
 semionotids 183, 206, 210, 212, 214–16, 233–4, 236, 240, 244, 267, 270, 275, 277, 295, 297
Semionotus 394
 sensory canals of cheek 313–16
 skull roof 324–5
 snout 267–71
Seymouria 322
Sigaspis 324
 silurids 392
Sinamia 183, 244
 Sinemurian 238, 247, 278
 sinus superior 216, 227–8, 242, 246
 snout 185, 259
 sphenotic 211–12, 214–15, 240, 242, 244
Soederberghia 270, 366
 solum nasi 267
Somniosus 301
Sphenodon 306, 360 —
 spinal nerve 363
 first 208
 fourth 379
 plate 375–6
 spino-occipital nerves 198, 210
 spiracle 211, 238–40, 242–4, 246, 277, 291, 301, 310–11, 313
 spiracular canal 211, 216, 238, 242–4, 246, 271, 277, 301, 395, 397
 cartilage 235
 cleft 244, 278, 291, 317
 diverticulum 242, 277–8, 283
 groove 181, 216, 238–9, 242–4, 246, 271, 273–9, 283, 286,

- 292, 395–6, 402
 ossicles 243, 352
 pouch 243, 310
 recess 242
 rudiment 301
 sense organ 244
 slit 181, 283, 286, 317
 spiraculo-hyomandibular recess 283
 splenial 333, 336, 402
 squaloids 403
Squalus 212, 235–6, 239–41, 247–8, 298–9, 301, 368
 squamation 386, 388–92
 squamosal 312, 316, 395–6
Squatina 235–6, 239–41, 360
 stegotrachelid palaeoniscid 181
 Stegotrachelidae 181
Stegotrachelus 312, 374, 398
 stenioellids 336
 stephanodont teeth 336–7
 sternohyoideus muscle 346
Stomiahykus 306
Strepsodus 366
 stromatoporoid reefs 176
Strunius 253
 walteri 77B
 surgeons 233, 243, 277, 333, 339, 353, 381, 392
Styracopterus 394
 subcephalic muscles 271, 273, 279–80
 subcranial muscle 197
 'subholosteans' 398
 sublingual rod 360
 submandibular 339, 341–2, 404
 submarginal 341
 subopercular 338–9, 342–3, 403
 suborbital 312, 398
 shelf 254, 263, 298–9
 subotical shelf 240
 subtemporal fossa 212, 232, 245
 superficial ophthalmic nerve 237–8, 247, 251, 255
 foramina 225–6, 230, 239–40, 249
 superior oblique 254, 265–6
 rectus 249
 superognathal 337
 supra-angular 94, 182, 331–3, 397–8
 supracleithrum 125, 339, 368, 370, 374
 supracoracoid foramen 379, 381, 402
 supraethmoid 267
 supraglenoid buttress 380
 foramen 378, 380–1
 supramaxilla 396, 399
 supraneurals 268, 363, 368, 386
 supraoccipital 189, 199, 201, 203, 206–8, 216
 supraorbital 311, 404
 sensory canal 225, 254–5, 260, 263, 270, 312, 316–7, 324–5, 404
 vein 249, 251
 supraotic cavity 201, 247
 suprapharyngobranchial 118, 218, 233–5, 301, 362–3, 403
 articulation 233–4, 348
 first 218, 233–4, 346, 348
 second 233, 348–9
 suprapharyngohyal 352
 suprapharyngomandibular 301
 suprapterygoid 306
 process 211
 supratemporal 80–3, 291, 311, 317–18, 320, 322
 commissure 312, 318, 324
 suprascapula 380
 surangular 331, 333, 336
 swimbladder 396, 403
 symplectic 357–9, 396, 399
 synapomorphies summarized 395–406

 tabular 311–12, 320–1
Tamiobatis 203–4, 207, 210, 235, 240, 301
Tarpon 394
Tarrasius 386
 tectals 271, 404
 tectum 267
 teeth 260, 263–4, 271, 273, 278–9, 286–7, 292, 295, 307, 310, 331–2, 336, 403, pl. 4
Tegeolepis 339, 394
 telencephalon recess 226, 249
 Teleostei 400
 teleosts 183–4, 189, 191, 195, 197, 203, 205–6, 211–12, 214, 216, 228, 233–4, 236–8, 240, 243–7, 249, 251–2, 265, 267, 270, 275–8, 295, 297, 299, 305–7, 312–13, 322, 324, 332–3, 339, 343, 346, 352, 357, 359–63, 365–6, 368, 374, 378–80, 382, 384, 386, 388, 392, 394, 397
 temnospondyls 243, 311, 322, 333, 336, 365
 temporal sensory canal 239, 244, 287, 311–12, 317–18
 series 312
 tentacle blastemas 295
 tesserae 183–4, 336
 Tetrapoda 400
 tetrapods 183, 185, 204, 206–7, 243, 247, 270–1, 275–6, 299, 301, 307–8, 310–13, 320–2, 324, 332–3, 336, 341, 361, 365, 368, 370, 380–1, 392, 400, 403–4, 406
Thursius 368
 tooth plates 271, 273, 278–80, 283, 292, 333, 336–8, 344, 346, 348–9, 356, 361–2
Torpedo 247–8, 251, 313, 324
 torpedoes 235
 trabeculae 188, 204, 235, 241, 247–8, 267, 293, 295, 299
 transpalatine 307–8
 transverse bolster of basisphenoid 214, 249
 process 190–1
 transversi ventrali 403
Trematosaurus 324
Triazeugacanthus 253
 trigeminal canal 218, 230, 237–8, 248–9, 251
 foramen 18, 195, 211, 214, 218, 224, 227, 237–8, 248
 nerve 207, 227, 238, 248, 251, 327
 ganglion 236–9
 mandibular branch 298, 313, 327
 maxillary branch 298
 root 218, 251
 trigeminofacialis chamber 235–40, 244
Trimerorhachis 312, 324
Tristychius 241
Triton 306
 trochlear nerve 224, 226, 248–9
 foramen 225, 249
 truncus infraorbitalis 266
 trunk muscle 197, 199, 209
Turseodus 365
Tylostotriton verrucosus 76E

 uncinat processes 398–9
Undina 298, 306
 Upper Carboniferous 365
 Jurassic 232, 234, 236, 243
Uranolophus 271, 273, 275, 279, 295, 311, 324, 392, 394
 urodeles 208, 299, 306, 308, 360, 362
 utricular recess 18, 218, 227–8, 237–9, 251
 urohyal 362
Urolophus 301
Uronemus 297, 321

 vagus canal 188, 197, 199, 201, 203, 210–11, 217, 228
 foramen 189–91, 201, 212, 233–4, 396
 nerve 199, 216–17, 245, 316, 348
 pharyngeal branch 216–17
 supratemporal branch 216–17, 233
 valvula 395
 vaterite 395, 397
 ventral ethmoid 267, 295
 ventral + marginal fin muscles 379, 381, 383
 ventral otic fissure 181, 185, 188–9, 191, 195, 199, 204–6, 210–11, 214, 222, 224, 234, 241, 249, 271, 273, 275, 277, 279
 ventrolateral sinus 251
Vermicomacanthus 374–5
 vertebrae 191, 366
 first 208
 vertebral joint 205
 vertical pit-line 57, 61–2, 287, 291, 313–14

- vestibular fontanelle 185–6, 188–9,
192, 199, 203–5, 215–17,
249, 348
- visceral arches 301
- origin 235
- vomer 50, 222, 260, 264, 271, 273,
293–8, 404
- Watson's palaeoniscid A 194
- Watsonichthys* 251, 307, 310, 344,
374
- Watsonulus* 203
- Western Australia 176, 182
- Australian Museum 181
- Westoll-lines 392
- Whiteia* 211, 295, 324, 332–3
- Wijdeaspis* 207, 240
- warrooensis* 185
- Wildungen 182
- Wimania* 211–12, 233, 273, 298
- xenacanth sharks 202, 207, 403
- Xenacanthus* 203–4, 210, 235, 239–
40, 298, 301
- Xenomystus* 206
- Youngolepididae 177, 404
- youngolepidids 273, 277–8, 311, 404
- Youngolepiformes 400
- Youngolepis* 204, 210, 239–40, 247,
249, 266, 274–6, 278–80,
298, 311, 400, 404
- zygal plates 192, 194–6, 207, 227